The effects of fertilisers, particularly foliar applied, on the potato plant's tolerance of attack by the potato cystnematodes, *Globodera rostochiensis* and *G. pallida*

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The effects of fertilisers, particularly foliar applied, on the potato plant's tolerance of attack by the potato cyst nematodes, *Globodera rostochiensis* and *G. pallida*.

Ivan Geoffrey Grove BSc (Hons)

A thesis submitted in partial fulfilment of the requirements of the Open University for the degree of Doctor of Philosophy

Submitted **April 1999**
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Harper Adams University College in collaboration with Hydro-Agri UK Ltd and IACR-Rothamsted

Declaration

This thesis was composed by the author and is a record of work carried out by him on an original line of research. All sources of information are shown in the texts and listed in the references; all help given by others is indicated in the acknowledgements.

None of this work has been presented in any previous application for any degree or qualification.

Signed ....(Ivan G Grove)

The effects of fertiliser, particularly foliar applied, on the potato plant's tolerance of attack by the potato cyst nematodes, *Globodera rostochiensis* and *G. pallida*.

By I. G. Grove

Abstract

Potato cyst nematodes, PCN, cause major yield loss in commercial potato production. One of the mechanisms of yield loss cited is a reduction in the uptake of the major nutrients nitrogen (N), phosphorus (P) and potassium (K). For the work described in this thesis, it was hypothesised that nutrient application via the foliar route could by-pass the PCN-damaged plant root system, ameliorate the PCN-induced nutrient deficits and increase plant yield and tolerance of PCN attack.

None of the three nutrients investigated (N, P, K) was individually shown to limit plant growth or yield of PCN-infected plants. However, plant nutrient concentrations were affected by PCN-infection: N and K concentrations were reduced by 30 days after planting (DAP); N and P concentrations were significantly reduced by 56 to 61 DAP; but N and P were significantly greater in plants by 104 DAP. PCN-infection also significantly retarded plant emergence, and reduced plant growth and yield in all investigations.

Applying placed liquid fertiliser increased the plant nutrient concentrations but did not increase tuber yield significantly. Applying one third of the recommended fertiliser quantity as foliar-applied nutrients effectively replaced seedbed application, increased the nutrient concentrations within the plants and gave equivalent or higher tuber yields than in plants receiving all of the fertiliser in the seedbed. Applying all of the recommended quantity of N in the seedbed at planting did not increase early plant growth, although it did redress some of the PCN-induced nutrient deficits, and appeared to aggravate the yield loss associated with PCN infection.

Applying foliar N on five occasions, at approximately 14-day intervals, produced small but consistent yield improvements by increasing ground cover and leaf area index. Yield improvements were also seen where applications included either foliar K within the foliar N application, or when one early foliar P application was made with the first of four or five foliar N applications. Applying foliar P alone on four occasions at approximately 5-day intervals from early post-emergence, or five occasions at approximately 14 day intervals from tuber initiation, reduced plant growth and yield. However, even where nutrient concentrations within PCN-infected plants were increased to the same level as, or greater level, found in relatively PCN-free plants, no significant plant growth benefits occurred. Therefore, it is postulated that a separate mechanism, i.e. phytohormone imbalance, may be solely or additionally responsible for the poor growth of PCN-infected plants. Field and glasshouse investigations showed contrasting effects of nutrients, especially foliar-applied, and nematicide applications, and highlighted the greater suitability of field experimentation for these types of investigation.

The Diagnosis and Recommendation Integrated System (DRIS) was investigated as an alternative diagnostic tool to aid the identification of nutrient disorders. Although no remedial nutrient applications were made as a result of the findings from this method, it suggested that P was most limiting for early plant growth and, in contrast to the statistical analysis which showed no limitations, K was most limiting for plant growth later in the season.

In conclusion, it is suggested that foliar nutrient applications can benefit the growth, yield and tolerance of PCN-infected plants, but that plant tolerance may benefit further if nutrient applications match the requirements of the plant as shown by plant nutrient analyses.

Dedication

This thesis is dedicated to my mother, father and sister. Thank you for your encouragement and support throughout my life.

Acknowledgements

My son Richard, always interested, supportive and proud of my work.
My nephew Christopher, who provided the entertainment to break up the work.

My fiancée Sarah, for checking the final draft, putting up with my late nights and the weekend working and, for getting me out on the hills when it was time for a break.

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Victoria Cruxton, Alex Raeside and Clive George of the Science laboratories at Harper Adams who gave me their time when I learned new techniques and put up with my sense of humour.

Statement of advance studies

During the tenure of this project, in addition to performing and reporting the experiments in this manuscript the author has also:

- completed an M.Sc. unit in statistical procedures
- completed a course in technical writing skills
- attended weekly research seminars at HAAC
- received training for electrophoresis, spectrophotometry and high performance liquid chromotography analysis and in the use of the Institute of Hydrology neutron probe.
- poster presented at : The Association of Applied Biologists - Offered papers in nematology, Linnean Society, London, England (December, 1997).
- presented papers at:

The 25th Anniversary celebration of a Mezator college in Hungary, for which I received an award for the best scientific presentation (Dec 1997).

The 24th European Society of Nematologists conference, Dundee, Scotland (3rd - 9th August, 1998).

The Association of Applied Biologists - Offered papers in nematology, Linnean Society, London, England (December, 1998).

Other:

- attended both nematology and related research conferences
- been an active member of the HAAC Nematology group
- given lectures and practical sessions: identifying potatoes infected by PCN.
- led practical sessions on PCN extraction, quantification and species identification by IEF.
- demonstrated the use of the neutron probe to HND and BSc students.
- acted as advisor and internal examiner for one B.Sc. Investigational project.
- written standard operating procedures (SOPs) for PCN species determination using isoelectric focusing and quantification of PCN root invasion of potatoes.

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1. Introduction

1.1 The justification for this research

The potato crop (*Solanum tuberosum* ssp *tuberosum*) is ranked as the fourth most important food source worldwide (Ulrich, 1993) with over 18 million hectares (ha) and an annual gross output of 295 million tonnes, giving an average yield of 16.1 t/ha (FAO, 1997). In the UK there were 13,395 registered growers in 1996, producing a total of 7.2 million tonnes of potatoes from 177,000 ha and an average yield of 40.8 t/ha (FAO, 1997; PMB, 1997). As an important food source, with each person in the UK consuming 101.7 kg/year (PMB, 1997), and an important crop for growers, any problems which reduce the crop yield will also reduce growers' financial returns and the food supply available to the population. One such problem is the potato cyst nematodes (PCN) which Evans & Haydock (1990) suggest are responsible for yield losses in the order of 10% of the total world production. The mere presence of PCN in soil prevents the use of the land for potato seed production because most countries operate clean seed programmes and where soil is heavily infested it is inadvisable to plant potatoes as substantial damage may occur.

The efficient management of field infestations of the two species of PCN, *Globodera rostochiensis* and *G. pallida,* requires careful planning and the implementation of suitable control measures, e.g. the use of nematicides, which can restrict PCN hatch and immobilise juveniles in the soil (Whitehead, 1998), and the use of resistant cultivars, which restrict PCN multiplication. However, in the absence of nematicides an infected potato crop will still produce tubers but yields will be dependent on both the severity of PCN infection and the cultivar's inherent ability to withstand infection by PCN, its 'tolerance'. These tolerance traits are complex and are affected by many variables, including environmental factors (Evans & Haydock, 1990). The importance of the tolerance was shown when Evans & Franco (1979) grew ten potato cultivars in the presence of PCN but without the protection of a nematicide. At an average density of 29 eggs/g soil of *G. rostochiensis*, the cultivars Maris Piper and Désirée yielded 60% and 14%, respectively, of their yield capability in PCN-free soil. Thus, in the event of restrictions being placed on the use of nematicides, such as those arising from environmental concerns, knowledge of the tolerance of PCN of potato cultivars and any methods which may improve it will be essential to maintenance of potato supply.

The research in this thesis is aimed at amelioration of an acknowledged mechanism of yield loss attributed to PCN infection, i.e. the reduced uptake of the macro nutrients nitrogen (N), phosphorus (P) and potassium (K) (Trudgill, Evans & Parrot, 1975a, 1975b; Trudgill, Parrot, Evans & Widdowson, 1975c; Trudgill, 1980). Several attempts have been made to alleviate such nutrient stress, with the aim of improving the PCN tolerance of the plant, by applying higher rates of fertilisers (Trudgill, 1980, 1987; Villagarcia & Franco, 1984). Few, however, have been successful or met with consistent results. There is evidence to suggest that calcium and magnesium uptake is also affected (Trudgill *et al.*, 1975c; Fatemy & Evans, 1986a, 1986b; Haverkort, de Ruijter, Boerma & van de Waart, 1996) but N, P and K were the nutrients considered most relevant to this research for two reasons: a) they have already been shown, in some cases, to be severely affected by PCN infection, and b) as Watson (1963) points out, these three elements have large general effects on plant growth that vary with the amount supplied over a wide range, whilst the other elements have more specific biochemical roles and relatively small effects on growth within a narrow range of supply.

1.1.1 Research hypotheses

The core hypotheses used in this research are that a) fertiliser applications by the foliar route, by-passing the PCN-damaged root system, could ameliorate nutrient problems and increase the plant's tolerance of PCN attack, and b) amendments to the timing or placement of soil applied fertiliser could improve the availability of N, P and K and, therefore, the tolerance of the potato plant to invasion by PCN. The strategies employed in the research were 1) to use applications of foliar N, P and K to identify the most limiting of these nutrients and then focus on the application criteria for the most critical in order to ameliorate any limitations that had been imposed on the plants; 2) to determine whether a particular seedbed fertiliser application technique was more suited to PCN infected plants; and 3) to investigate whether manipulation of the quantity and timing of the seed-bed nitrogen requirement of the crop enhanced early or late growth of PCN infected plants. The experimental work was mainly in the form of field experiments, except for one major glasshouse experiment. The field approach was adopted as previous work in this area has shown conflicting results when treatments applied in glasshouse conditions have failed to elicit similar responses in the field, e.g. (Trudgill, 1980).

1.2 The potato crop

First domesticated in South America, specifically in the Andean regions of Peru and Bolivia, the potato was introduced into Europe at around 1570 and England circa 1596/97 (Hawkes, 1992a). Belonging to the family Solanaceae, in which are documented 75 genera and over 2000 species, the commercial potato crop belongs to the single species *Solanum tuberosum* L. in all but a few cases. The potato crop, is largely one of temperate regions and is now grown widely around the world and increasingly in tropical latitudes (Kay, 1987). In the UK the potato crop can be classified into three main maturity classes: earlies, second earlies and maincrops, with maincrops also being divided into early maincrop and late maincrop.

1.2.1 Crop use and markets

In the UK, the majority of potatoes are produced for human consumption because of their nutritional characteristics of high carbohydrate and low fat contents. The tubers are composed of 70-80% water and 20-30% solids, with the solids consisting of 16-20% carbohydrates (of which 95% is starch), 0.1-0.2% fats, 2.5-3.2% nitrogenous compounds, 1.2-2.2% protein (being part of the nitrogenous compounds), 0.8-2.0% minerals (low in sodium and high in potassium) and 0.6% fibre (Bajaj, 1987). The solids or dry matter content of tubers normally falls within the 20-30% range and is very important in relation to their cooking characteristics. The nutritional qualities of the potato also make it a good livestock feed which, according to Beukema & Van Der Zaag (1990), over one third of the world's potato production in 1982 was used for. The UK crop is normally grown for the ware market, domestic or catering use, processing or pre-packing, or to produce immature potatoes for canning. Specialised growers also provide seed for the potato industry and there are industrial outlets for use of potatoes for starch and alcohol manufacture.

1.2.2 Crop growth

The potato plant is as a herbaceous freely-branching, dicotyledonous, perennial plant of approximately 30-100cm in height. The plant produces one or several stems with alternate pinnately compound leaves, which are made up of three or four main pairs of oval leaflets, secondary and tertiary leaflets and a terminal leaflet (Kay, 1987; Cutter, 1992). The final number of leaves and branches are dependent whether individual cultivars have determinate or indeterminate patterns of growth (Anon, 1993). Flowers are produced near the ends of branches with colours dependent on cultivar. True seed, fruit, is produced in a round berry of approximately 1.5-2 cm diameter. The root system, made up of fine fibrous and adventitious roots, normally extends to a depth of 40-50 cm but can extend to a depth of one metre where there are no compacted soil layers to restrict growth (Kay, 1987; Beukema & Van Der Zaag, 1990). Stolons are produced below the soil surface shortly before the emergence of the plant, initially at the basal nodes of the hypocotyl and then progressively upwards throughout the life of the plant (Dean, 1994). The majority of stolons, however, are produced during the early stages of plant development. The tips of the stolons swell to form the tubers, which enlarge over the growing season. Plant growth initially is very dependent on the nutrient supply from the mother tuber and it is not until the leaf surface area has attained 200-400 cm^2 that photosynthesis can supply sufficient carbohydrates to maintain plant growth. It is suggested that, once the plant can supply its own carbohydrate requirements from photosynthesis, excess carbohydrates from the leaves are exported back to the mother tuber, which also provides a supply of minerals to the plant (Moorby, 1968). There are several growth stage keys which attempt to describe the growth of the potato plant but each is flawed in one way or another. Jefferies & Lawson (1991) discuss these schemes and propose a version which describes plant development better than most others.

1.2.3 Components of yield

Millard & Marshall (1986) list four factors that govern the yield of potatoes: radiation interception; the conversion of intercepted radiation to dry matter; partitioning of dry matter between tubers and the rest of the plant; and regulation of tuber dry matter content. These take into account such factors as leaf area index (LAI) and leaf area duration (LAD), and nutrient and water availability, by their effects on the four components. Husbandry factors such as cultivar, seed rate, pest control, soil structure and the planned length of the growing period will all also influence the four components of yield.

The LAI determines the amount of solar radiation intercepted by the crop. MacKerron & Waister (1985) and Gunasena (1969) suggest that a LAI of 3 will allow interception of 95-98% of the incident radiation and that this is the minimum LAI required to allow maximum tuber bulking rate. Burstall & Harris (1983), however, suggest that a LAI of 6 is required to reduce soil water loss from evaporation and thus maximise yield from the improved soil water status. The actual leaf area index attained by a potato crop is affected by the plant density, stem and leaf number and leaf angle (Allen & Scott, 1992). The LAD summarises the length of time that the photosynthetically active leaves are available to utilise the photosynthetically active radiation (PAR). As with LAI, the LAD can be influenced by several factors including planting date, physiological age of the seed, and haulm senescence or destruction for harvesting. With regard to the effects of the LAD and LAI on yield, however, it should be noted that in the UK the amount of incident radiation available for interception is greatest in the months of May to July. Therefore, Allen & Scott (1992) suggested that a crop canopy which can utilise as much of the radiation in this period as possible will produce higher yields than a smaller canopy in May-July but which extends into the autumn. Gunasena & Harris (1971) demonstrated that there are linear relationships between LAD and total yield, or LAD and dry matter yield.

The rate of photosynthesis has an important effect on the bulking rate of the tubers. It is determined by several factors including respiration, radiation, CO_2 concentration around the leaves, temperature and the amount of leaf area available for photosynthesis. The optimum temperature for photosynthesis in potatoes is suggested as 20 to 25°C (Beukema & Van Der Zaag, 1990). However, at temperatures greater than 25°C a negative effect on production occurs which is said to arise from reduced net assimilation due to increased respiration, changes in the partitioning of assimilates to favour stem and branch growth, with a reduction in leaf area, and a corresponding reduction in tuber yield (Dwelle *et al.*, 1981; Kay, 1987).

1.2.4 Yield potential

The average harvested yield for the UK maincrop is given by the Potato Marketing Board (Anon, 1996c) as 41.7 t/ha for 1995 and 44.8 t/ha in 1994, the harvested yield being lower than actual yield as conventional harvesters are fitted with webs which allow small tubers to remain in the field. The potential yield of a potato crop was researched by Evans & Neild (1981) who demonstrated that total tuber yields of between 70 and 94 t/ha were possible. Their work showed that achievement of these yields required greater quantities of N and P fertilisers than were recommended and that an adequate water supply was essential.

1.3 Crop nutrition

In their native environment, plants grow and produce storage organs, i.e tubers in potatoes and seed in cereals, without the benefit of additional fertiliser nutrients. However, agricultural practices are aimed at maximising the yield of useful plant parts and to this end additional nutrients are supplied to crops in various forms of fertiliser materials. This is by no means a recent innovation as Millar (1955) refers to the writings of Sir Kenelur Digley (1669), where crop yields were doubled by the application of saltpetre (potassium nitrate), and also to the writings of the historian Xenophon (430 to 355 BC) which describe the ploughing under of green plants to enrich soils. Today, the achievement of the highest possible crop yield, attained at an economically justifiable level, requires particular attention to both the requirement of the crop and the application of fertiliser nutrients. The following discussion of the nutrients N, P and K should not be taken to mean that these nutrients are the only ones considered important in the nutrition of the potato crop -merely that they are the nutrients under consideration in this research. For discussion of the importance and roles of other essential nutrients the relevant works include Mengel & Kirkby (1987) and Marschner (1995).

1.3.1 Mineral nutrition of the potato

The first stages of potato plant growth are seen as sprouts from the mother tuber. The nutrients for this growth, pre-planting, come entirely from the mother tuber. Once the seed tuber is planted the mother tuber continues to supply nutrients but the sprout forms roots which increase the supply of mineral ions (Moorby & Milthorpe, 1975). The importance of nutrient supply to the pre-emerged plant from sources other than the mother tuber was shown when increasing concentrations of mineral ions in the soil solution increased both the rate of emergence and the numbers of stems appearing above the ground (Moorby, 1968). The daughter tubers, once formed, quickly become the dominant sink for nutrients and, when mineral uptake from roots is insufficient to supply all of the plant's requirements, nutrients are actively translocated from the haulm to these tubers. The mother tuber, although supplying many of the nutrients to the plant initially, imports carbohydrates throughout the season (Moorby, 1968), demonstrating a continued active role in the functioning of the plant. As the plant continues to grow throughout the season there is a continued uptake of N, P and K which, according to Gunasena (1969), reaches a maximum at 128 days after planting (DAP). Ezeta & McCollum (1972), however, suggest that N uptake is greatest at 95-137 DAP and K uptake at 95-116 DAP, during which periods the crop takes up 2.5 kg N and 6.6 kg K/ha per day. Phosphorus, which is taken up in relatively lower quantities than N and K, decreases in concentration in leaves, stems and tubers throughout the season. Overall figures for the daily uptake rates of N, P and K by a healthy potato crop are given by Ezeta & McCollum (1972) as 1.7 to 5.1 kg N/ha/day, 0.14 to 0.26 kg P/ha/day and 1.3 to 2.6 kg K/ha/day. These figures are mean values taken from many cultivars grown around the world and represent a total accumulation over a 128 day growing period of 218 to 653 kg N/ha, 17.9 to 33.3 kg P/ha and 166 to 333 kg K/ha.

As an indication of nutrient requirements of a potato crop achieving a 30 t/ha tuber yield, where nutrient removal is related to tuber yield only, with no plant growth accounted for, Harris (1992) cited three sources which, when extrapolated to 30 t/ha of fresh tubers suggested nutrient removal of : 71.4 to 80.4 kg N, 15.9 to 18.6 kg P and 118 to 140 kg K. As reserves of these nutrients vary considerably between soils, the quantities of additional N, P and K required for second early and maincrop potato production in the UK take soil reserves into account and are recommended by ADAS (Anon, 1994) : 50-240 kg N/ha for soil indices 2 to 0, 0-350 kg P/ha for soil indices over 4 to 0; 0-350 kg K/ha for soil indices over 4 to 0 (the K recommendations are based on the requirements of the crop to produce a tuber fresh-weight yield 40 t/ha).

1.3.2 Nutrient roles and effect on crop growth and yield

i) Nitrogen

Nitrogen is considered as potentially the most yield limiting of all nutrients. This is because most soils are unable to hold or build up reservoirs of this nutrient and only soils of high organic matter content have good supplies of organic N (Harris, 1992). The necessity for N arises from its role as a component in proteins, amino acids, amino enzymes, nucleic acids, chlorophyll, alkaloids and purine bases, all of which are essential for plant growth.

Dyson & Watson (1971) reported an increase in tuber yields from applications of artificial N and demonstrated that leaf and stem growth were increased from early in the season. According to Vos & Biemond (1992), the rate of leaf appearance is only slightly affected by N supply but the rate of leaf expansion and apical branching, and thus the total number of leaves on the plant, can be related to N supply. Dyson & Watson (1971) also reported that where N was applied the LAI reached 2.5-3.0 and the LAD was increased by 125%, whereas plots receiving no N attained an LAI of only 1.0. The effects of the increased LAI and LAD are important as Harris (1992) suggests that there is a direct relationship between intercepted radiation and total dry matter yield. Where nitrogen is applied, therefore, an increase in leaf area and duration will give positive yield benefits (Millard & Marshall, 1986; Beukema & Van Der Zaag, 1990). Millard & Marshall (1986) suggest that N applications of 150 kg/ha are sufficient for maximum tuber yields and demonstrated that applications of N greater than 250 kg/ha increased the partitioning of N to the haulm at the expense of the tubers. Excessive rates of N are also suggested to cause reductions in the dry matter content of tubers and high levels of reducing sugars, proteins and nitrates in the tuber (Beukema & Van Der Zaag, 1990) and potential delays in the onset of tuber initiation (Anon, 1993). Gunasena (1969) has shown that late applications of N can depress yields, but Gunasena & Harris (1971) have demonstrated the beneficial effects of delayed or split N applications, which reduce N loss by leaching. There was no direct effect of N applications on the rate of photosynthesis in work carried out by Firman & Allen (1988) but it was reported that in some cases N applications can reduce the photosynthetic rate due to an increased canopy size and consequent increased water stress and stomatal resistance.

Neeteson (1989) gives a yield response curve for potatoes receiving N applications ranging from zero to 400 kg N/ha (Figure 1.1).

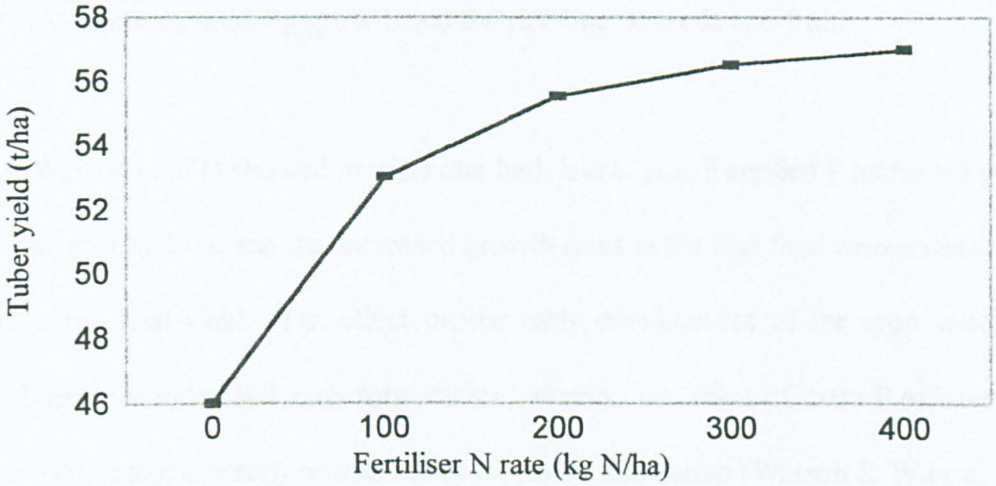

Figure 1.1 The yield response of potatoes to applications of fertiliser nitrogen (redrawn from Neeteson (1989) with permission of the Royal Netherlands Society of Agricultural Science).

In a series of experiments on 14 silty soil sites, Berryman *et al.* (1973) reported that an application of 156 kg N/ha (as sulphate of ammonia, 21% N) gave yield responses of from 5 to 20 t/ha, with the smaller responses occurring from applications to the heavier silt soils. These response were much greater than those reported by Boyd & Dermott (1964), who gave 4 t/ha as the average yield response to a similar N application (151 kg/ha as sulphate of ammonia, 21% N) in 124 experiments. The latter report, however, encompassed a greater number of experiments and a much wider range of soil types, including sandy loams, clay loams and silt loams.

ii) Phosphorus

Although the concentrations of P found in plants is low in comparison to those of N and K, it is still considered as a major element. It is necessary for DNA and RNA nucleotides and is an essential factor in the many sugar phosphates involved in photosynthesis and in other metabolic processes due to its presence in ATP, ADP, AMP and pyrophosphate, an essential energy source for activities within cells (Salisbury & Ross, 1992). Phosphorus is important for root development, seedling growth and the ripening of seeds and fruits.

Dyson & Watson (1971) showed in trials that high levels of soil applied P increased yield by 9% and leaf area by 17%, and that increased growth rates in the first four weeks were carried through to the final yield. The effect on the early development of the crop arises from improved leaf area index and early tuberisation, whereas the effect of extra P of later stages of crop growth is to cause early senescence of the leaves and haulm (Watson & Wilson, 1956). Phosphorus is reported to increase root growth relative to shoot growth whereas N increases shoot growth relative to root growth. The SAC (Anon, 1993) indicate that applications of P_2O_5 can increase the rate of haulm growth, tuberisation and early bulking and thus give a higher early yield but, except soils deficient in P, there is no yield benefit in the later stages of growth. The yield increase from P application has been shown by Locascio & Rhue (1990) to be influenced by phosphate form. Yields were significantly lower with diammonium phosphate (DAP) than those achieved with liquid polyphosphate, liquid orthophosphate or triple super phosphates. It is perhaps worthy of note, however, that although the yield increase was lowest with DAP the plant and shoot tissue P concentrations were highest from this P source. From the crop nutrient application and removal rates given earlier, it can be seen that, although similarly high rates of applications can be recommended for both P and K, there is substantially less removal of P. The need for high application rates for P is due to its relative immobility in soil, which moves to plant roots solely by diffusion (Fageria, 1992). Phosphorus is taken up by plants as either $H_2PO_4^-$ or HPO_4^{2-}. Where soil pH is below 7.0, $H_2PO_4^-$ becomes dominant in the soil with HPO_4^{2-} almost absent at pH 5.0. At pH > 7.2 HPO_4^{2-} becomes the dominant form in the soil (Fageria, 1992).

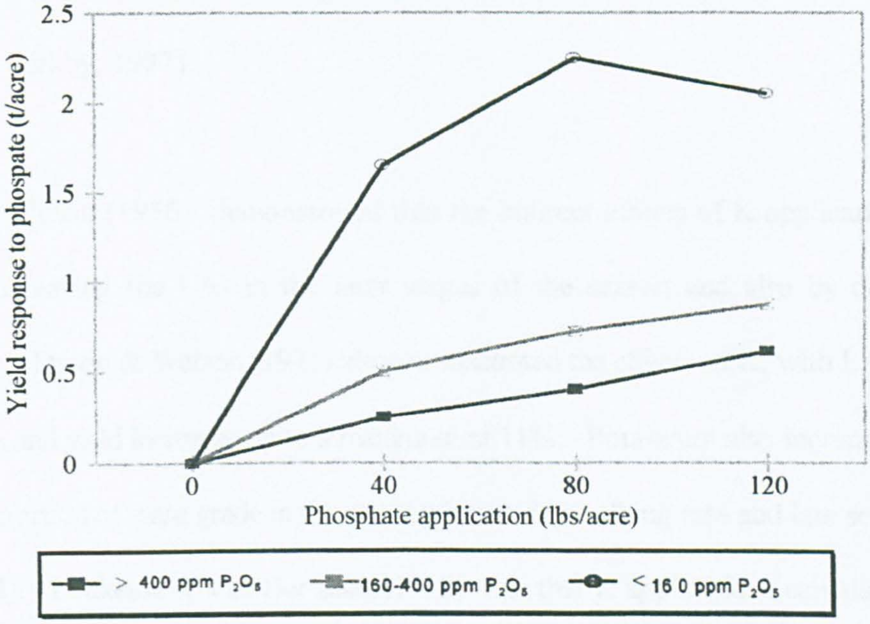

Figure 1.2 The yield response of potatoes to applications of P_2O_5 at three levels of soil P_2O_5 status (reproduced from Birch *et al.* (1967) with kind permission of the Cambridge University Press).

Birch *et al.* (1967) demonstrated that potato yield response to P application rate was affected by the initial soil P_2O_5 levels (Figure 1.2). They also found that the response varied between years but mainly affected medium to large tuber production. This agrees with Berryman *et al.* (1973) who found average tuber yield responses to applications of P fertiliser of 5 t/ha at soil indices 1 and 2, 3.3 t/ha at index 3 and around 1.3 t/ha at indices 4 and 5. It was further noted, however, that in one series of experiments an interaction occurred between applications of N and P which resulted in yield reductions. A similar effect has also been reported by Boyd & Dermott (1967) who found an average reduction of 0.3 t/acre.

iii) Potassium

Potassium, unlike N and P, is not a structural component of any proteins, carbohydrates or other organic compounds. The functions of K in plants are the activation of enzymes, regulation of cell water content, maintenance of cell turgor, maximising rates of cell expansion, control of transpiration through its functions in the stomatal guard cells, and roles in the transport of photosynthates and sugars to the tubers, where they are converted to starch (Mengel & Kirkby, 1987).

Watson & Wilson (1956) demonstrated that the indirect effects of K applications on yield were by increasing the LAI in the later stages of the season and also by delaying crop senescence. Dyson & Watson (1971) also demonstrated the effects of K, with LAD increases of up to 9% and yield increases up to a maximum of 11%. Potassium also increases tuber size and the proportion of ware grade in the crop by improving bulking rate and late season growth (SAC, 1993). Beukema & Van Der Zaag (1990) note that K applications can also reduce dry matter content and thus dry matter yield. In fact, the relationship is even more complicated as the SAC (1993) found that where muriate of potash is used, tuber dry matter yields are less than where sulphate of potash is used.

A direct effect of K applications on yield (Figure 1.3) was demonstrated by Birch *et al.* (1967). Berryman *et al.* (1973) reached similar conclusions that yield is dependent on the initial levels of K_2O found in the soil, with greater responses to K application in soils poor in K and only small reponses occurring in soils rich in K, i.e. the silts. The work by Gunasena & Harris (1971) agrees with this and also suggests that split applications of K can be beneficial over single applications made early or late.

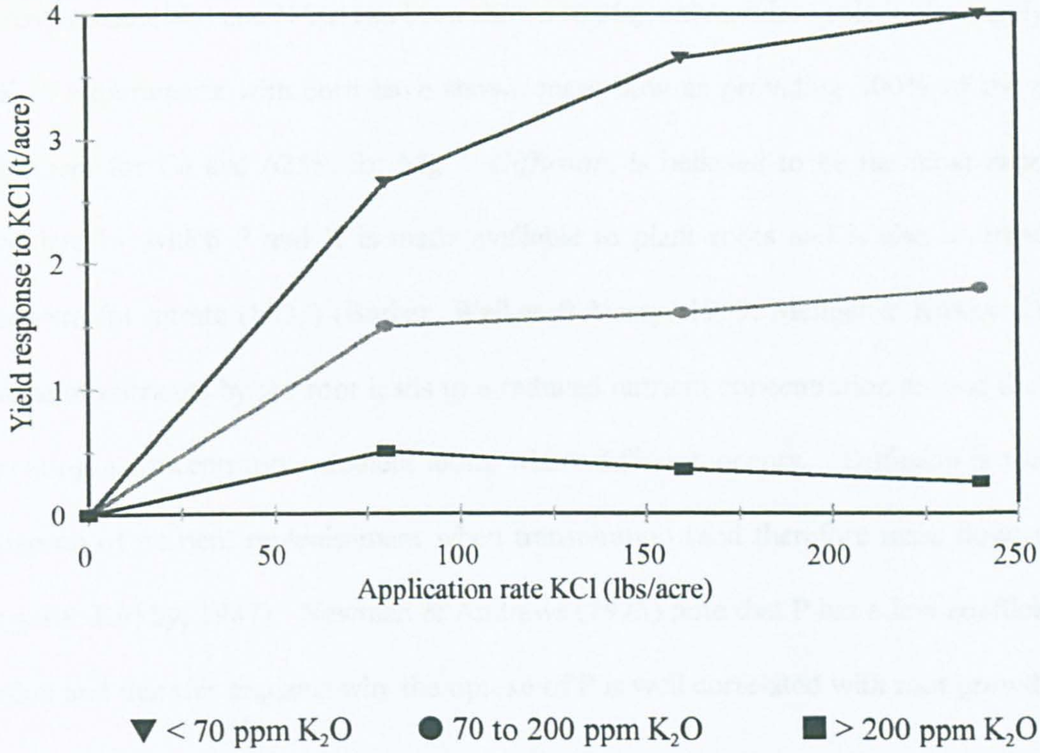

Figure 1.3 The yield response of potatoes to applications of K_2O at three levels of citric soluble soil K_2O (redrawn from Birch *et al.* (1967) with kind permission of the Cambridge University Press).

1.3.3 Factors affecting nutrient availability and (nutrient) uptake

Barber, Walker & Vasey (1963) describe three methods by which plant roots intercept soil nutrients: interception, mass flow and diffusion. *Interception*, occurs when roots grow through the soil and the cells of the root surface come into contact with nutrient elements bound onto soil colloids. There is then an exchange of ions: H^+ released from root cells is exchanged for other cations, e.g. K^+, where contact between roots and soil colloids occur. It has been suggested that root interception would achieve only 3% contact with the nutrients available in soil, but experiments with corn showed that 6% of the crop's requirement for N, 10% of P and 9% of K was accounted for by this method. *Mass flow*, is the movement of water, and thus nutrients within the soil water, to the plant roots thought to be driven by transpiration. It is one of the main methods by which plant roots are supplied with calcium (Ca), magnesium (Mg) and N but has been shown to play only a minor role in the supply of P and K. Experiments with corn have shown mass flow as providing 500% of the plants requirement for Ca and 625% for Mg. *Diffusion*, is believed to be the most important mechanism by which P and K is made available to plant roots and is also an important mechanism for nitrate (NO_3^-) (Barber, Walker & Vasey, 1963; Mengel & Kirkby, 1987). Removal of nutrients by the root leads to a reduced nutrient concentration around the roots so creating a concentration gradient along which diffusion occurs. Diffusion is the main mechanism of nutrient replenishment when transpiration (and therefore mass flow) is low (Mengel & Kirkby, 1987). Newman & Andrews (1973) note that P has a low coefficient of diffusion and that this explains why the uptake of P is well correlated with root growth.

i) Nutrient form and availability in soil

The principal forms of available N in soils are ammonium-N (NH_4^+) and nitrate-N (NO_3^-). The quantity available largely depends on the organic matter content of the soil as this contains N in both the amino (proteins) and heterocyclic (N bases of nucleic acids) forms, which are converted first to NH_4^+ and then NO_3^- by microorganisms within the soil. Soil factors influence the rate at which these processes occur, e.g. temperature and moisture.

Phosphates in soils available for plant nutrition are classed in three main fractions: 1) phosphate in soil solution, 2) phosphate in the labile pool, and 3) phosphate in the non-labile fraction. The phosphate in the soil solution is simply that which is dissolved in the soil solution. Phosphate in the labile pool is that which is held on soil surfaces, consists mainly of calcium phosphates, and is in rapid equilibrium with soil solution phosphate. The last phosphate fraction, non-labile, is insoluble and is released only very slowly into the labile pool. Most of the phosphate found in soils is in the form of orthophosphate, at levels ranging from 0.002 to 0.15% P, of which mineral soils contain 20-80% in the organic form. The main source of K^+ for plants is the weathering of the clay fractions within soil. Soil potassium can also be divided into three fractions: 1) as a structural element of soil minerals, 2) K^+ adsorbed in exchangeable form to soil colloids such as clay minerals and organic matter, and 3) K^+ present in the soil solution. Potassium released by weathering of minerals is dissolved in the soil solution and can be taken up directly by plants or be adsorbed by soil colloids.

The potato crop can tolerate, and grow well, in soils of pH 5.0 (Bolton, 1971). When mineral soils reach such a low pH level, however, the cation exchange sites of the clay fraction, which normally hold Mg and Ca cations, are occupied by aluminium ions. These sites then become strong adsorbers of phosphate and molybdate (Marschner, 1995) leading to a reduction in the availability of phosphates. When the pH of the soil is allowed to fall below 4.8 Beukema & Van Der Zaag (1990) suggest that problems from calcium deficiency occur and restricted crop growth results from an increase in the uptake of toxic quantities of the more available aluminium (Al), manganese (Mn) and iron (Fe). Liming or an increase in soil pH above 5.0 can also have a detrimental effect, this time on the uptake of K by potatoes (Harris, 1992): lime-induced K deficiency occurs as the result of increased K adsorption onto the soil cation exchange sites (Bolton, 1971). Rao & Rains (1976) showed that NH_4^+ is taken up in higher quantities at a neutral pH whilst the uptake of NO_3^- is greater at lower pH values.

ii) Root growth and morphology

There are three primary functions of roots: 1) anchoring the plant, 2) synthesis of phytohormones and organic compounds, and 3) absorption and translocation of water and nutrients, which is the only factor of interest in this thesis. The absorption and translocation of water and nutrients is mainly influenced by root morphology, which is itself genetically controlled, but is also affected by environmental factors such as the soil atmosphere, mechanical impedance and by plant nutrient status. The soil atmosphere must contain sufficient oxygen as this is important for root growth. Where anaerobic soil conditions exist a reduction in root growth can occur. Mechanical impedance can restrict the passage of roots through the soil, which results in reduced rooting depth and, consequently, a reduced potential for water and nutrient accumulation. Roots grow more extensively in dry than in wet soils, as the roots search out water, and this also produces a denser root system. The number of root tips is very important for the uptake of Ca, Mg and Fe as these are mainly absorbed by young root tissues. The root hairs play an important role in P uptake which is dependent on root hair length, due in part to the exploitation of the less accessible soil particles. The potential nutrient uptake of a root system is dependent on the number of roots per plant or the quantity of roots per unit volume of soil and probably greatly exceeds the nutrient requirement of the plant. This relatively high nutrient uptake potential therefore enables the plant to absorb sufficient quantities of nutrients even when nutrient availability is low. Young plants have the greatest requirement for nutrients and the uptake per metre of root is considerably higher in young plants than later in the season (Mengel & Kirkby, 1987; Marschner, 1995). The morphology of roots is, therefore, very important in nutrient uptake especially as nutrients are depleted from the soil around them, creating depletion zones especially of P, which depend more on diffusion rather than mass flow for access by roots.

1.3.4 Nutrient movement, remobilisation and translocation within the plant

The movement or translocation of nutrients around the plant, especially to and from leaves, can be of major importance during several stages of crop growth: seed germination; periods of insufficient supply from the soil during vegetative growth; the period before leaf fall

(Marschner, 1995); and, in relation to this thesis, when nutrients are applied to the leaves. During seed germination, the stored mineral nutrients are remobilised and translocated in the phloem and/or the xylem to the developing shoots and roots, until root uptake of nutrients begins. In potatoes, it has been shown that the mother tuber initially supplies all of the nutrients for sprout growth but that the supply of nutrients from the soil is important even before emergence of the plant (Moorby, 1968; Moorby & Milthorpe, 1975). During the vegetative growth period, when there may be insufficient supply of nutrients from the soil or low soil moisture levels may occur, the remobilisation of nutrients from mature leaves to new growth is very important. Where deficiency symptoms occur in young leaves or apical meristems the nutrient deficiency is said to reflect poor phloem mobility or an inability to convert the nutrients to a mobile form within the mature leaves (Marschner, 1995). The remobilisation of nutrients during the formation of seeds and storage organs is also very important as nutrient uptake generally decreases at this time. The extent of the remobilisation is dependent on several factors: 1) the specific requirement of the seed or storage organ for the nutrient, e.g. potato tubers have a large requirement for K but relatively small requirements for N and P; 2) the mineral nutrient status of the vegetative parts; 3) the ratio between the vegetative mass (source size) and number and size of the seeds or storage organs (sink size); 4) the nutrient uptake rate by the roots during the reproductive stage (Marschner, 1995).

Nitrogen is readily translocated and remobilised within plant tissue. The main forms in which N is translocated are as NO_3^- and amino acids, with the latter dominating in supplies to young expanding leaves (Milthorpe & Moorby, 1969). Where N supplies are inadequate from the soil, proteins in mature leaves are hydrolysed and the amino acids translocated to the young growing plant part (Mengel & Kirkby, 1987). The cycling of N translocated through the xylem has also been shown to be important in barley plants, whereby 79% of that passed up through the xylem is retranslocated as reduced N back to the roots, at which point 21% of that is incorporated into the root tissue and the remainder cycled back in the xylem to the shoots (Simpson, Lambers & Dalling, 1982).

Phosphate is readily mobile in the plant, can be translocated to upper plant parts or to root tips after uptake, and can be moved from older to younger leaves when required. Primarily taken up (at physiological pH) as $H_2PO_4^-$ it may remain as inorganic phosphate (P_i), esterified as a simple phosphate ester (e.g. sugar phosphate) or attached to another phosphate (e.g. in ATP). After initial absorption by root cells 80% of the phosphate is actively metabolised into organic compounds (e.g., hexose phosphates and uridine diphosphate) after only 10 minutes (Jackson & Hagen, 1960), but Marschner (1995) suggests that it is subsequently released again as P_i into the xylem.

Potassium is taken up as the univalent cation K^+. It is very mobile between cells, within tissues and throughout the plant via the phloem and xylem. Potassium is not metabolised and forms only weak complexes which are readily exchangeable. Where soil supplies of K^+ are limiting, the nutrient is retranslocated from mature leaves and stems to younger tissues (Marschner, 1995). The high mobility of K^+ throughout the plant is due mainly to the high permeability of membranes to this cation (Mengel & Kirkby, 1987). Although the nutrients Ca and Mn are not covered in this review it is worth noting that with the exception of these two nutrients all other nutrients are readily translocated around the plant to redress any shortfall in their supply from the soil medium.

1.3.5 Types of fertiliser

Across the world, the nutrient requirements for potato production are met from various sources which include animal manures, seaweeds, green manures and inorganic (artificial) fertilisers. In this research project, however, only nutrients supplied from inorganic fertilisers are of interest. Solid fertilisers come in various forms which include powders, granules, prills or crystalline forms. Powders are uncommon today because they have poor spreading characteristics. Granules are formed from powders, with each granule of the same composition and contain three or more elements, including N, P and K. Prills are made by the rapid cooling of a molten fertiliser sprayed down a tower and, until recently, they contained only one nutrient. The crystalline fertiliser forms are normally either fragments of compacted solids, which are of variable shape, or true crystals which are uniform in shape. Granular and crystalline fertilisers can be supplied as 'Blends' which are mixtures of two or more elements contained in individual particles, or 'Compounds' in which each particle has the same composition of elements (Dyson, 1993).

Liquid fertilisers are produced as solutions or suspensions in which one or several nutrients may be present. In solutions, the nutrients are dissolved in water and the concentration is dependant on the water solubility of the nutrient. The suspensions hold finely ground fertilisers in suspension within a water mass. The solution is at present the most widely used of the two forms but, suspensions have a higher potential concentration of nutrients as solubility is not a factor (Dyson, 1993).

1.3.6 Fertiliser application method

The most common method of fertiliser application is the broadcasting of solid fertilisers across the soil surface before planting or after planting as a top dressings. These solids can also be 'placed' by the use of specialised application equipment. Knittel (1988) suggests that crops using wide row spacings benefit from the placement of P and N (as granules) through improved efficiency of the nutrients. The placed P is more efficient because there is a reduced contact between P and the soil which results in less P adsorption onto the soil, reducing 'lock up' (Knittel, 1988) which can lead to as much as 15% greater efficiency (Beukema & Van Der Zaag, 1990). Cooke (1949) demonstrated the benefits of placed P by achieving equivalent yields from potatoes when 40 kg/ha P_2O_5 was placed or 60 to 120 kg/ha P_2O_5 was broadcast. The optimum placement of fertilisers is suggested to be in two bands, one 50 cm below and another 50 cm to the side of the seed tuber.

Liquid fertilisers are normally injected at planting with the aid of specialised equipment mounted on the potato planter. The fertilisers can be injected after planting but care must be taken not to move the seed out of place in the ridge, or place the fertiliser too close to the seed tuber. Research carried out by Lewis and Kettlewell (1992) suggested that placed liquid fertiliser solution increased yields in the >60 mm grade and also increased leaf area, plant dry weights and phosphorus concentration within the plant.

An alternative approach to applying fertilisers to the soil is the application of fertiliser solutions to plant foliage. Rectifying trace element deficiency is the most common use for foliar fertilisers. However, NPK sprays are used for high value crops, such as ornamentals or vegetables, and are used regularly in Hawaii for pineapple and sugar cane (Gray, 1977; Hanway, 1988). Using this method to supply all of the crop nutrient requirements can, however, be both expensive (Dyson, 1993) and problematical. The Potash Development Association suggests that the leaf is incapable of taking up the high quantities of K required to meet the demands of the potato crop (Lidgate, 1992).

1.3.7 Foliar fertilisers

There are several problems associated with foliar nutrient applications which cause concern and this explains why the reliance on solid or liquid seedbed fertilisers remains. These problems include: the need to apply the nutrients in several doses, as only low rates of application are possible in any one spray; marginal or severe leaf burn if excessive doses are used; and the high cost per unit of plant nutrient. Potato yields can be increased with foliar NPK sprays (Gray, 1977) but, in general, the benefits to most crops are inconsistent.

i) Uptake of foliar nutrients

The absorption processes influencing the movement of solutes and nutrients into a leaf are not greatly different from those found in roots (Gray, 1977). The roots of a plant however, unlike the leaf, exist in an environment which brings them into contact with a varying continuum of available nutrients, and roots possess fewer solute barriers than are found in leaves. To supply nutrients to a plant through the leaf, therefore, brings problems of matching nutrient supply with demand and also requires an understanding of the composition of the leaf. The initial barrier to solutes passing into the leaf is the layer of epicuticular waxes. These are excreted by the epidermal cells and consist of long chain alcohols, ketones and esters of long chain fatty acids. The next barrier is the cuticle itself, which consists mainly of long chain fatty acids termed cutin, but the cuticle is also impregnated intracuticularly with epicuticular waxes which have chemical and physical gradients running from the hydrophobic outer surface to the more hydrophilic inner surface. The cuticle is between the epicuticular wax and a cutinised layer which consists of a cellulose skeleton incrusted with cutin, wax and pectin. Within the cuticle there are small hydrophilic pores, of less than 1nm, which occur at a density of approximately 10^{10} cm^{-2}. These pores are lined with fixed negative charges which increase in density from the outside of the cuticle to the inside and thus create a gradient for cation movement. Low molecular weight solutes such as urea, which is uncharged, or NH_4^+, are believed to pass into the leaf by this route. Anions such as NO_3^- are repulsed from this region at low concentrations but their uptake is not thought to be restricted when they occur at high concentrations. Synthetic chelated nutrients, formed from metallic cations which have reacted with a protecting colloid to form an electro-neutral complex, are too large to pass through the small hydrophilic pores. The entry points into the leaves for these nutrients are hydrophilic pores of different permeability characteristics, found around the stomatal guard cells and trichomes (Marschner, 1995).

Foliar nutrients, once deposited in solution on the leaf, have a limited period in the aqueous phase (Gray, 1977). Drying of this solution or rain wash-off within 24 hrs of application can therefore reduce or prevent nutrient uptake. When the leaves are turgid, the cuticle is more permeable and nutrient absorption is facilitated, whereas leaves under moisture stress are very resistant to foliar nutrient uptake. The uptake and translocation of a nutrient can also be restricted if the nutrition of the plant is already being met adequately from the roots. Clarkson & Scattergood (1982) demonstrated that the rate of uptake of foliar applied P uptake was twice as high in a P-deficient barley plant as was observed in barley plants with no P deficiency. It was also shown that more translocation of P from the leaves, especially to the roots, occurred in plants deficient in P. The rate of uptake of foliar nutrients, however, is reduced in ageing leaves where thickening of the cuticle and a decrease in the metabolic activity is occurring (Marschner, 1995). Alexander (1986) suggests further factors that affect uptake, including differences in epicuticular wax thickness between cultivars, osmotic potential of the root medium and several other environmental and spray solution characteristics. Lewis & Kettlewell (1993) demonstrated that the uptake of foliar P applied to potatoes was greatly influenced by cultivar, air temperature and humidity but that windspeed had no effect, and that phosphorus uptake decreased linearly in relation to decreased water availability. The uptake of the nutrient alone is not the sole criterion for its usefulness as a foliar fertiliser: the inability of the plant to translocate Ca from mature leaves to other areas of the plant severely restrict its suitability.

ii) Materials and their suitability as foliar nutrients

The main materials used for foliar application of N is urea, with ammonium phosphates and ammonium sulphate as alternatives (Bowen, 1993). Urea-triazone solutions have also been reported to be very useful for foliar applications (Clapp, 1993) as they are capable of containing higher concentrations of nutrient without causing the associated foliage damage (scorch) seen with other N products; concentrations of 5.8 to 7.1% N can be used with no risk of scorch to potatoes. The main sources of P are from mono- and di-ammonium phosphate, referred to as MAP and DAP. MAP contains approximately 12% N and 60% P_2O_5 whilst DAP contains about 21% N and 50% P_2O_5. Phosphate alone can be applied as polyphosphates, which are superior for liquid foliar sprays as they do not form insoluble precipitates with iron or other heavy metals, which create blockages in jets of liquid fertiliser distributors. Polyphosphates are, however, not widely available. Barel & Black (1979) screened 32 different compounds for suitability as foliar nutrients and found that orthophosphoric acid, one of the most suitable, caused excessive scorch on corn at concentrations greater than 0.5% P. The main source of K is suggested by Gray (1977) as muriate of potash, KCl. Chamel (1988) gives the suitability of various K compounds ranked in descending order of their rate of uptake: potassium carbonate (K_2CO_3) > potassium chloride (KCl) = potassium nitrate (KNO_3) > potassium hydrogen phosphate (KH_2PO_4) > potassium sulphate (K_2SO_4).

Gray (1977) listed the desirable characteristics of a foliar nutrient spray as: a low salt index to minimize damage to plant cells from osmotic pressures; high solubility of the fertiliser material to reduce the volume of solution required for each application; high purity of materials to eliminate impurities that might interfere with spraying or that might cause adverse foliage reactions; and polyphosphate sources are preferred over ortho-phosphates as they cause less scorch. Barel & Black (1979b) found that reduced leaf burn occurred on soybean when sucrose was included in applications of urea and to some extent phosphate in the form of orthophosphoric acid. Leaf damage from applications of P and K together is also likely to be greater than the sum of the damage caused by separate applications. No benefits arose from altering the pH of solutions over the range of 2-10 for orthophosphates but absorption decreased with increasing pH for tripolyphosphate.

iii) Timing of foliar applications

The first requirement when applying foliar nutrients is that sufficient leaf area is available to intercept the nutrient being applied. Beyond this, applications can either be remedial, to correct nutrient deficiencies, or planned to coincide with periods of rapid growth, which is when leaves are most effective at absorbing nutrients. In the potato crop, Alexander (1986) suggests that foliar N, P and K fertilisers are best applied during the stalk elongation phase. Applications should not be made to plants suffering from moisture stress or under bright sunlight and low humidity, as found around mid-day, as this can lead to excessive leaf burn (Gray, 1977; Hanway, 1988). High humidity, low temperature and low wind speed also prevent rapid drying of the applied spray droplets (Chamel, 1988), which can increase the period over which the nutrients are absorbed (Price, 1982).

iv) Foliar nutrition of potatoes

Bowen (1993) found that where foliar P was applied in addition to seed bed P a yield increase of 1.9 t/ha was obtained but where foliar P was applied without seedbed P the yield increase was 2.7 t/ha. Not all of the experimental results were significant and the experiments were carried out on soils of moderate or high soil P status. Lewis & Kettlewell (1992) made a foliar application at tuber initiation of 10 kg P_2O_5/ha, as a mixture of ortho- and poly-phosphates, and found no significant effects from the application. The soil analysis for this experiment, however, showed P levels of 57ppm corresponding to ADAS index 4 (Anon, 1994), which may have been too high for a significant response to occur, as the best responses come from foliar fertilisers when small amounts of fertiliser are applied to the soil (Mukherjee & De, 1968)

Mukerjee & De (1968) compared the response in potato yields to soil and foliar applications of N and P. The first experiment was not described clearly but, taken literally, the N and P were either applied all by soil or all by foliar application. When used as a foliar spray, the yields from foliar applications of 40 kg N/ha were significantly higher than 80 kg N/ha applied to the soil. Foliar applications of P at 15 and 30 kg P/ha produced yields equivalent to the 30 & 60 kg P/ha applied to the soil. The data from a second experiment suggest that applications of 120 kg N/ha in combination with 80kg P/ha, applied half to soil and half by the foliar route, increased yields by 19.5% over that achieved with all soil applications. When only one quarter of full rate was applied at planting and a further one quarter by foliar application the yield achieved was similar to that achieved with all fertiliser applied to the soil.

In research on foliar application of urea, Bailey *et al.* (1992) found no yield increases or decreases from applications of foliar urea tested against a range of split applications of soil applied ammonium nitrate. They did, however, suggest a potential environmental benefit as the foliar applied urea was taken up more efficiently and nitrogen recovery was increased slightly when half of the nitrogen was applied as a sequence of foliar sprays. Where the foliar applications were made at urea concentrations of 31.3%, high rates of foliage scorch were noted which may have masked any yield increases which could have occurred. Dixit & Sharma (1985) found no yield advantage over split applications of soil applied urea N when two foliar applications of 10 kg N/ha were used to complete a programme of N nutrition. Chaudhury *et al.* (1984) studied various aspects of potato crop growth in relation to the method and timing of N application. The foliar treatments studied produced yields significantly higher than the mean of those achieved with soil applied urea. The benefits from the foliar treatments seemed to arise from more rapid top growth and an increased leaf area duration. In more recent research, Millard & Robinson (1990) outlined the benefits of foliar applied urea as slightly improving yields and tuber N contents (especially in potato crops grown over a long growing period) and suggested that foliar urea has environmental benefits in reducing N losses as a greater proportion of the N is utilised than with broadcast applications of N.

1.3.8 Determination of plant nutrient status and deficiency

For plants to grow and yield in a satisfactory manner it is essential that their nutrient requirements are being met. The identification of these nutritional needs can be achieved through the use of soil tests, field and glasshouse experiments, examination of foliar symptoms, whole plant or leaf analysis, soluble nutrient (sap) tests, or biochemical and physiological tests (Bould, 1983; Smith, 1986; Benton Jones, Wolf & Mills, 1991). Soil tests are used to determine the nutrient supplying capacity of a soil, and therefore aid fertiliser application decisions, but cannot identify whether the crop is utilising the available nutrients. Sap tests, which quantify nutrients in the ionic or soluble form within the plant, are suggested by Marschner (1995) as offering a better characterisation of stored reserves and also the physiological availability of a nutrient within the plant. Biochemical and physiological tests are based on their roles in plant metabolism and it is possible to establish the status of nutrients in the plant by assaying for enzyme activity, enzyme reactivation and metabolic products Besford (1975), Johnson, Whittington & Blackwood (1976), and Besford (1978). For the purpose of this research thesis, however, only visual and chemical analysis is discussed.

i) Visual diagnosis

Visual diagnosis can be used to identify nutritional disorders in plants but several points are noteworthy: 1) symptoms tend only to be visible when the plant is very deficient; 2) symptoms can be species specific and diagnosis should be made with specific species references in mind; 3) agrochemical use and air pollutants can cause similar symptoms; 4) where several nutrients are deficient the symptoms for the combined deficiency can be different to the symptoms that occur from a single nutrient deficiency (Bould, 1983).

ii) Chemical analysis and interpretation

Chemical analysis of whole or specific plant parts provides values for the total concentration of a nutrient or a specific fraction of the nutrient, e.g. total N or NO_3^- N. One of the most common plant parts used for diagnosis of nutrient status is the leaf, which Bould (1983) suggests is a principle site of metabolism where changes in nutrient supply are well reflected, and which correlates well with crop performance and yield.

The interpretation of the measured values into specific nutrient status diagnoses is based on 'critical concentrations' (Ulrich, 1993), 'critical nutrient levels' Okhi (1987), and 'critical deficient level' (CDL), standard values, or sufficiency ranges (Benton Jones *et al.*, 1991). Ulrich (1993) suggests that the critical concentrations are a convenient reference point for assessing the nutritional status of plants. These were defined as the nutrient concentrations that are a) just deficient for maximum growth; b) just adequate for maximum growth; or c) separating the zone of deficiency from the zone of adequacy (Ulrich, 1952). Overall, the differences in 'critical' terminology, except for critical nutrient ranges, are small, and all are based on the nutrient concentration at which the plant can achieve only 90% of its potential dry matter yield (Figure 1.4) thus making the choice of term largely academic. The definition of plant nutrient status or disorders using critical concentrations, however, is viewed with scepticism by Marschner (1995) because the values are gauged by interrupting nutrient supplies to young glasshouse grown plants. This was shown by Burns (1992) to lead to a much higher value than those found in field grown plants. This argument, however, may be invalid as Smith (1986) suggests that the values reported for the 'critical concentrations' should not be taken as single specific or definitive values and that narrow critical ranges of nutrient concentrations should be used instead. Thus, if the critical concentration is treated as a narrow range, it would be no different to the 'critical nutrient ranges' (CNR) (which use transition zones) preferred by Benton Jones *et al.* (1991) and Marschner (1995), who both prefer CNR for its more flexible and useful guide to interpretation of nutrient status. Sufficient or adequate nutrient ranges, within which no restriction of plant growth should occur, are useful diagnosis guides. However, concentrations close to the lower values need to account for transitional states, when the status of the nutrient in question may alternate between the two states. To take account of such cases the quoted standards may include a 'low range' which falls between deficiency and sufficiency. Three examples (Table 1.1) outline typical levels of tissue nutrient concentrations in the fourth leaf from the plant tip (petioles plus blades) for field grown potatoes, mid season, late season and growth stage IV (tuber bulking).

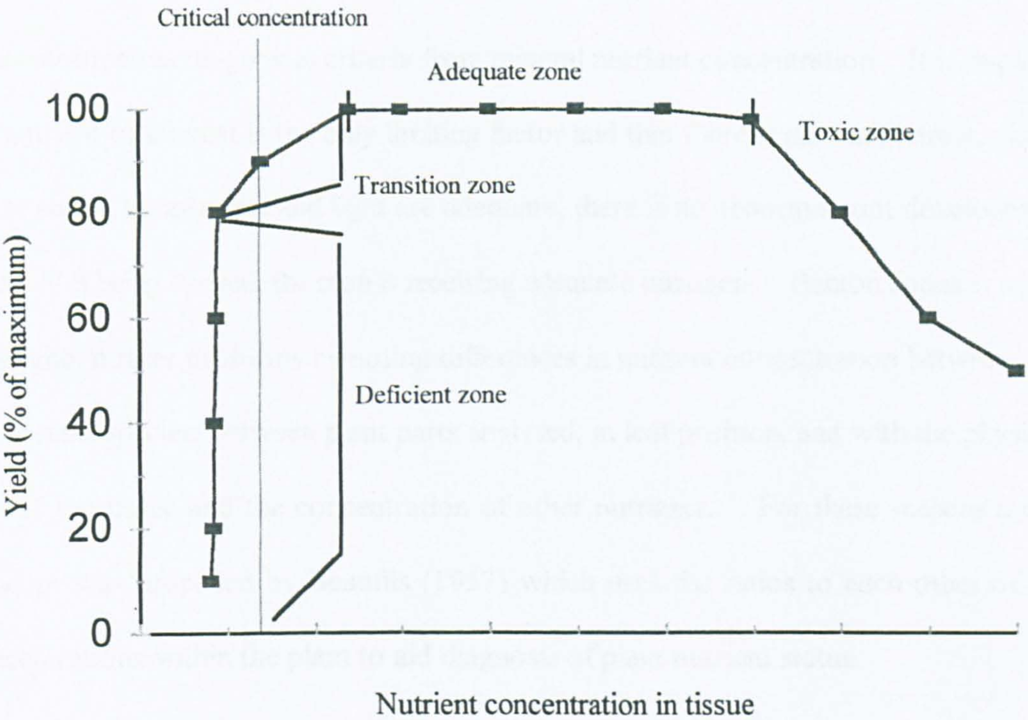

Figure 1.4 The zones of nutrient concentration within plant tissue and the derivation of the critical nutrient concentration (redrawn from Smith (1986) with kind permission of CSIRO Publishing, Australia).

Table 1.1 Typical percentage nutrient values of potato fourth leaf (petiole + blade) classed as sufficient for unrestricted growth at different growth stages.

		Growth parameter				
Reference		42DAE [a]	mid season	MidT [b]	GSIV [c]	late season
1	%N		3.51-4.50			3.00-4.00
2	%N				>3.50	
3	%N	4.0-5.0		3.0-5.0		
1	%P		0.26-0.75			0.25-0.40
2	%P				>0.25	
3	%P	0.2-0.4		0.1-0.3		
1	%K		3.51-5.10			6.00-8.00
2	%K				>3.5	
3	%K	3.5-5.0		4.00-8.00		

[a] days after emergence. [b] growth stage IV (tuber bulking). [c] tubers half grown.
1) Walworth and Muniz (1993), 2) Westermann (1993), 3)Reuter and Robinson (1986).

iii) Influences on the nutrient concentration within plant tissue

Smith (1986) highlights some of the problems associated with the use of critical nutrient concentrations as diagnostic criteria from mineral nutrient concentration. It is required that the nutrient of interest is the only limiting factor and that there is no water stress, disease or insect attack, temperature and light are adequate, there is no abnormal root development and, unless N is being studied, the crop is receiving adequate nitrogen. Benton Jones *et al.* (1991) highlights further problems by noting differences in nutrient concentration between cultivars of the same species, between plant parts analysed, in leaf position, and with the physiological age of the tissue and the concentration of other nutrients. For these reasons a different concept was proposed by Beaufils (1957) which uses the ratios to each other of nutrient concentrations within the plant to aid diagnosis of plant nutrient status.

iv) Nutrient ratios

The most common use of nutrient ratios is to describe the relationship of N, P and K fertilisers applied to a crop. The importance of the relationship is because different crops take up nutrients in different known ratios, e.g. cereals take up N, P and K in a ratio of 1:0.3:0.8 respectively, and the application of fertilisers should be aimed at maintaining this relationship to attain satisfactory yields (Mengel & Kirkby, 1987). In practice, the ratio of fertiliser applications alone is not sufficient to specify crop nutrient requirements as other factors such as soil nutrient status will affect the final quantities of fertiliser required. A ratio system that has been shown to be very useful in diagnosing plant nutrient disorders was proposed by Beaufils (1957) as a Diagnosis and Recommendation Integrated System (DRIS) (Sumner, 1977; Walworth & Sumner, 1987). The methodology determines the optimum nutrient ratios (nutrient norms), e.g. N/P, N/K and K/P, of nutrients measured in high yielding plants, which are then used as standards to determine which nutrients are limiting in low yielding crops of the same species. The ultimate goal of this system was to overcome the problems associated with the use of critical concentrations (as discussed in the previous section) and provide recommendations for the corrective nutrition of the soil to prevent similar nutrient limiting effects in the forthcoming seasons. Marschner (1995) suggests that the system may be very useful where large scale intensive cropping is carried out but is not a suitable method from which to make fertiliser recommendations for annual crops, low input crops or small scale farming enterprises. The problems with the recommendations for annual crops come mainly from the inability to supply readily available macro-nutrients, other than N, to plants analysed in that season (unless foliar nutrients are used). The recommendations are therefore normally suggested as corrective for the following season, as found in Benton Jones *et al.* (1991). Although some of the nutrient ratios have a physiological basis for their relationship, Smith (1986) suggests that this form of DRIS system is not suitable for use in Australia as several of the key ratios were not based on a recognised physiological relationship. Meldal-Johnsen & Sumner (1980) compared the DRIS system with both the critical concentration and sufficiency range methods for diagnosing nutrient disorders. Using field experimentation they found that in many cases all three systems compared favourably, but that the DRIS system successfully diagnosed limiting nutrients more often and, when these were redressed, resulted in higher yields.

1.4 The potato cyst nematodes

The potato cyst nematodes (PCN) are two species of soil living plant endoparasites. They are commonly referred to by several descriptive names: Eelworm, the Golden nematode of potatoes and the white or cream potato cyst nematode. Throughout this thesis they will be referred to by their specific names, *Globodera rostochiensis* Woll. and *G. pallida* Stone. or, where the species is not important, their acronym PCN.

1.4.1 Origin and development

Evans, Franco & de Scurrah (1975) suggest that both species of PCN, *Globodera rostochiensis* and *G. pallida,* originated from the Andean regions of South America where, according to Stone (1985), it co-evolved with the ancestors of the potato plant *Solanum tuberosum*. More recently, however, molecular analysis by Ferris *et al.* (1995) suggests that Mexico may be the centre of origin for the PCN. The first recognition of a cyst nematode specific to potatoes was in 1923 when a nematode population in Germany, previously thought to be a subspecies of the sugar beet cyst nematode *Heterodera schachtii*, was demonstrated to be the cause of 'soil sickness' in potatoes. This observation by Wollenweber then led to the first description (based on morphological differences) of a cyst nematode which specifically attacked potatoes, *Heterodera rostochiensis* Woll. (Mai, 1977). During the 1970s, Stone (1973) described a morphologically distinct variant as a separate species, *Heterodera pallida.* Further changes in the classification, however, occurred when the previously assigned subgeneric name *Globodera* Skarbilovich was elevated to generic rank (Mulvey & Stone, 1976). This classification made distinct groups of nematodes, most importantly *Heterodera, Globodera* and *Punctodera*, the potato cyst nematode species becoming *Globodera rostochiensis* and *G. pallida*. Loof & Bakker (1992) clarified the authorities to be used for bibliographic citations as:

G. rostochiensis (Wollenweber, 1923) Skarbilovich, 1959 (type species);

G. pallida Stone, 1973.

The two species, *G. rostochiensis & G. pallida*, which can be separated on morphological and/or other biological features, can be further classified into pathotypes or races.

i) Classification of PCN

Class	: *NEMATODEA*		
Subclass	: *Secernentia*		
Order	: *Tylenchida*		
Suborder	: *Tylenchina*		
Superfamily	: *Heteroderoidea*		
Family	: *Heteroderidae*		
Subfamily	: *Heteroderinae*		
Genera	: *Heterodera* (until 1976)		
	: *Globodera* (1976 onwards)		
Species	: *pallida*	&	*rostochiensis*
Pathotypes	: Pa1/2/3		Ro1/2/3/4/5 (Kort *et al.*, 1977)
	: $P_1A,P_1B,P_2A,P_3A,P_4A,P_5A,P_6A$		R_1A,R_1B,R_2A,R_3A (Canto & de Scurrah, 1977)
	:		Ro1,Ro3,Ro5 (Nijboer & Parlevliet, 1990)

Based on Hesling (1978) and Brodie *et al.* (1993).

a) Species identification

The 'golden' or 'white' PCN descriptions referred to earlier are based on observations of female colour during their development into cysts. These differences are not suitable for the distinction of the species as the cysts of both species eventually 'tan' to a similar colour. There are several current methods of determining the species make-up of populations. These are: morphological characteristics (differences are in the detailed morphology of the cysts or second stage juveniles rather than their gross morphology and are given by Evans & Rowe (1991)); Isoelectric focusing (IEF) of water soluble protein extracts as the two PCN species have been shown to have species specific proteins which migrate to precise isoelectric points(pI) (pI 5.9 for *Globodera rostochiensis* and 5.7 for *G. pallida* as 5.7 (Fleming & Marks, 1983; Marks & Fleming, 1985)); Polymerase chain reaction (PCR), which uses allele-specific amplification to identify PCN at the species level by using differences in the rRNA gene sequences of the two species (De Giorgi *et al.*, 1994); Restriction fragment length polymorphism (RFLP), by which *G. rostochiensis* and *G. pallida* can be differentiated due to differences in their genomes (Phillips *et al*, 1992); Enzyme linked immunosorbent assay (ELISA) species identification which is based on monoclonal antibodies that recognise the species differentially but which is still being evaluated and refined for commercial use (Evans *et al.*, 1995).

b) Pathotypes and races

The requirement for classification beyond the species level arose when populations of PCN were found in 1956, in Peru, which could overcome the PCN resistance known in potato plants at that time (Kort, 1974). This suggested that variations within PCN existed and thus a method of identifying and classifying the variants was required. Kort *et al.* (1977) proposed a 'pathotype' scheme which was extensively used (Stone *et al.*, 1986; Brodie *et al.*, 1993) and is stiil used in the UK National Institute of Agricultural Botany (NIAB) recommended cultivar lists (Anon, 1997) to classify PCN resistance in cultivars. Although an alternative scheme based on 'races' exists (Canto & de Scurrah, 1977), the Kort *et al.* (1977) 'International Pathotype Scheme' and the term pathotype are used to distinguish species variants within this thesis.

ii) Distribution

The current distribution of PCN includes most countries in which commercial potato growing is practised. Mai (1977) recorded that PCN were known from 47 countries worldwide, including most of Europe and countries as far apart as the USA, Russia, New Zealand and Japan. Not all of these countries, however, contain both PCN species or all of the pathotypes. In the UK, PCN have been recorded in all of the major potato growing areas but only Ro1, Pa1 and Pa2/3 have been found (Stone *et al.,* 1986). In a recent study using RFLP analysis Phillips *et al.* (1992) distinguished the pathotypes of *G. pallida* in the UK as Pa1 mostly confined to Northern Ireland and a small part of Scotland, Pa2/3 widespread in England, and a potentially separate pathotype in Luffness, Scotland. It is also suggested that *G. pallida* is becoming the dominant species in some areas (Stone *et al.*, 1986), which is probably largely due to the selection pressure from the availability of cultivars fully resistant to *G. rostochiensis* but not *G. pallida.*

1.4.2 Biology and life cycle

The potato cyst nematodes are sedentary endoparasites, incapable of independent long distance movement, which require a food source from internal tissues of a host. PCN exhibit a marked sexual dimorphism with distinct male and female forms. The females develop into spheres (cysts) either white or golden in colour initially, which become tanned to a darker brown colour as the cysts mature. The males are vermiform, cylindrical and elongate and without appendages for locomotion. The cysts of PCN are formed from the hardened female cuticle and contains the eggs of the next generation. The number of eggs in cysts varies but can range from 200-600 eggs/cyst (Anon, 1986). The eggs within cysts can withstand air-drying, unlike most other species of nematodes, and this explains how they can be transported over great distances and remain viable. They infect potato roots but Vovlas (1996) indicates that they are also found on the potato tuber. The life cycle is predominantly restricted to one per year in the UK but Evans (1969) reports experiments which demonstrate a small second generation occurring in August, on a maincrop cultivar.

The life cycle, Figure 1.5, can be divided into two distinct phases: a dormant phase and an active phase. The dormant phase occurs when the cysts remain in the soil for periods which may exceed 20 years in the absence of a host. In addition, there is a diapause which occurs soon after eggs are first fully formed and is a normal part of the life cycle, and therefore an obligate developmental arrest (Wharton, 1986). The eggs in the cysts contain second stage juveniles, J2s, and these remain dormant within the cyst until root exudates from a host crop stimulate hatching. A proportion of juveniles will hatch or die each year in the absence of a host, approximately 10-30% p.a. for both *G. rostochiensis* and *G. pallida* (Evans and Trudgill, 1992; Turner, 1996), resulting in a natural decline in the population. After hatching, the J2s are attracted to the host roots, the source of the exudate, and invade the root just behind the growing point and migrate intracellularly to the stele. When they reach the stele they induce the formation of groups of enlarged specialised feeding cells which form a syncytium and within 24 hrs the nematode starts feeding and begins to grow. The amalgamation of cells within the syncytia does not cause the cells to deteriorate and metabolic activity and the size of the nucleoli are increased in these cells. It is suggested that solutes transported in the vascular system enter the syncytia in a source/sink relationship, with the nematode feeding from the protoplasm. It takes approximately eight days for the nematode to reach the early 3rd stage juvenile and it is believed that sex determination takes place at this stage and depends on food supply (Trudgill, 1967). At 16 days, the 4th stage females are exposed at the root surface, whilst the males emerge from the root and are attracted by pheromones to the female in order to mate. The males may each fertilise several females but cease being active within 10 days in temperate conditions (Evans, 1970). As the female matures the embryos, deposited within her body, develop to the 1st stage juvenile (J1) and then to the J2 within the eggs before the female dies. Finally, the female body tans to form a protective cyst which will fall from the root, into the soil, and the cycle is ready to start again (Brodie *et al.*, 1993; Evans & Stone, 1977). The syncytium will normally provide sufficient nutrition for a maturing female until the embryonated eggs have developed, at approximately 45 to 60 days. In the absence of fertilisation, however, healthy females of *G. rostochiensis* have been found on the roots for periods of up to four months. Where resistant plants are grown, the formation of the syncytium is restricted or prevented (Zuckerman *et al.*,1971; Burrows, 1992). A time scale for the life cycle of *G. rostochiensis,* from hatching to maturity, is given by Hammond-Cosack *et al.* (1990) as:

In a non-resistant plant - penetration 6hrs, intracellular migration 12 hrs, cell selection and syncytium development 3 days from penetration, active feeding cell by six days, final female maturation 40 days.

In a resistant plant - as in a susceptible plant except that the process stops during syncytium development, the syncytium degenerates and the nematode dies without being able to attempt to initiate a new feeding site.

Hansen and Jakobsen (1985) used the number of day degrees above a base temperature of 5°C to calculate the development time of several species of cyst nematodes from around the world. They suggest that one generation requires 690 degree-days (5°C base) for full completion of the life cycle but the actual development stages require only 440 degree-days.

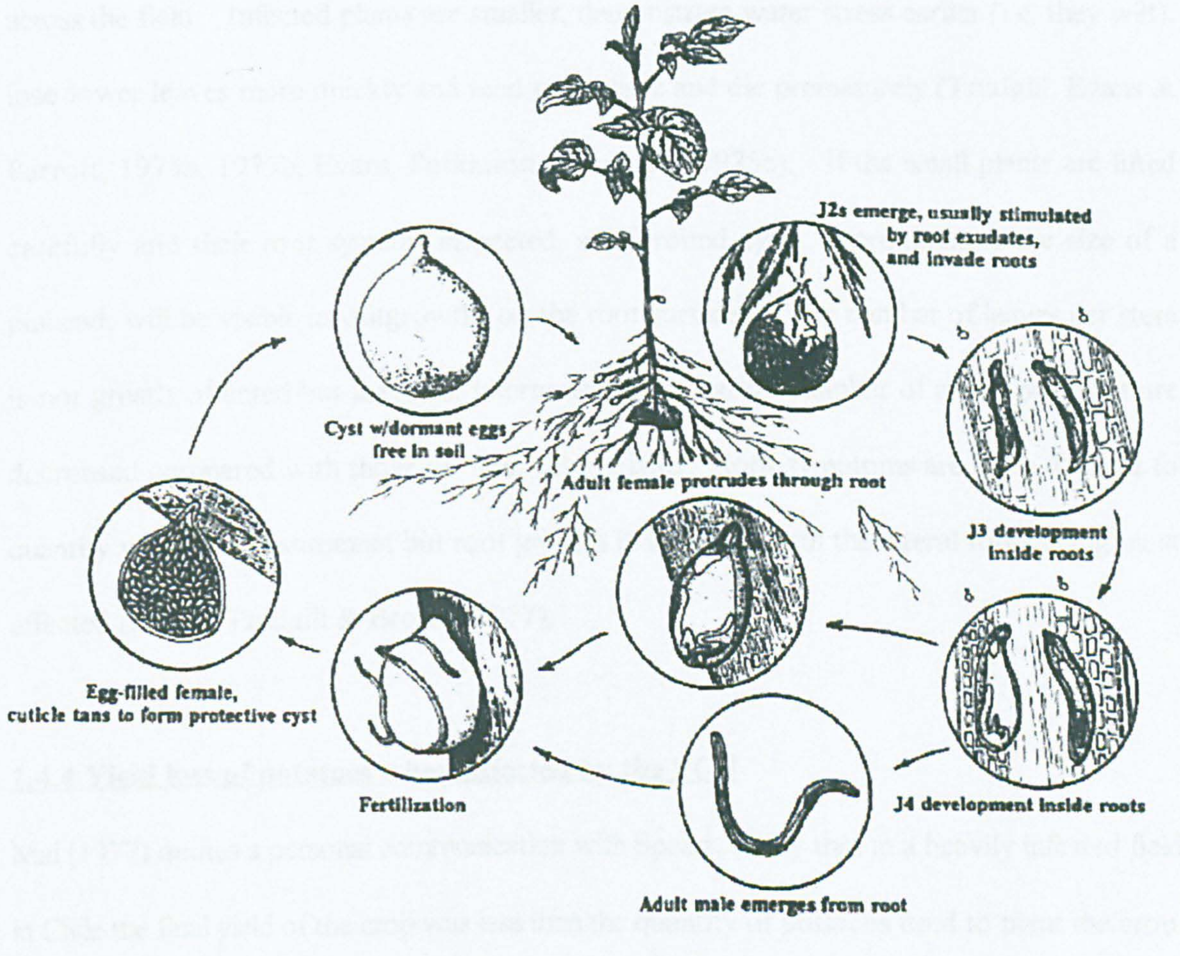

Figure 1.5 The life cycle of the potato cyst nematode (reproduced from Brodie *et al.* (1993) with kind permission of CAB International, Wallingford, Oxon).

Studies by Franco (1979) suggested that *G. pallida* is better adapted to the lower temperature range of 10 to 18°C, with greater hatching, and cyst and egg production per plant than *G.*

rostochiensis. There was little difference between the species at 20°C and *G. rostochiensis* hatched better at 25°C. The upper limit for development of *Heterodera rostochiensis* was given by Ferris (1957) as 29.4°C. Work in New Zealand by Foot (1978) gave similar results in that the optimum temperatures for multiplication for Ro1, Pa2 and Pa3 lay in the range 15 to 20°C.

1.4.3 Symptoms of PCN infection of potato plants

The symptoms of PCN attack in a potato crop are most apparent when PCN occurs in patches across the field. Infected plants are smaller, demonstrate water stress earlier (i.e. they wilt), lose lower leaves more quickly and tend to senesce and die prematurely (Trudgill, Evans & Parrott, 1975a, 1975b; Evans, Parkinson & Trudgill, 1975c). If the small plants are lifted carefully and their root systems inspected, small round cysts, approximately the size of a pinhead, will be visible as outgrowths on the root surfaces. The number of leaves per stem is not greatly affected but leaf size, internode length and the number of stems per plant are decreased compared with those of uninfected plants. Root symptoms are more difficult to quantify without measurement but root growth is inhibited, with the lateral roots being most affected (Evans, Trudgill & Brown, 1977).

1.4.4 Yield loss of potatoes when infected by the PCN

Mai (1977) quotes a personal communication with Spears, to say that in a heavily infested field in Chile the final yield of the crop was less than the quantity of potatoes used to plant the crop. On silt and peat soils in the UK, Brown (1969) reported yield losses of 2.01 t/ha per 20 eggs/g soil with *Heterodera rostochiensis*. Further work by Brown and Sykes (1983), with both *Globodera rostochiensis* and *G. pallida* on sandy soils, indicated mean yield losses of 2.75 t/ha per 20eggs/g with a maximum yield loss of 22 t/ha. Evans & Franco (1979) highlighted the differences in yield loss that could be expected between maincrop cultivars from ten different cultivars in PCN infected soil when the tuber yields ranged from 3.7 to 17.1 t/ha. Differences in yield loss at similar infestation levels are common; as Trudgill (1986) notes that yield losses are the result of an interaction with soil type, micro-organisms, husbandry, cultivars and yearly weather differences.

Loss of tuber yield from PCN infected potato plants results from complex interactions within the plant, caused by direct entry and invasion damage to the root, feeding by the nematode and physiological changes that occur because of this invasion. The actual parasitic feeding that takes place, however, was suggested by Trudgill *et al.* (1975a) to be a minor factor in the yield loss which only marginally affected the N status of the plant. This theory was later substantiated by Trudgill & Cotes (1983) who demonstrated that, with resistant cultivars, which prevent long periods of parasitic feeding, the subsequent loss of yield was due mainly to the initial damage caused to the root system and its effect on nutrient and water uptake. Evans *et al.* (1977) demonstrated that PCN affect the root system by causing reductions in both the number of lateral roots and the root density below the potato ridge. Haverkort *et al.* (1994) have since confirmed this by reporting experiments in which root growth between 30-100 cm was greatly reduced. This major mechanism of yield loss was suggested to be due to the slow initial root growth in the top soil whilst N was present, and the failure of roots to develop beyond the topsoil layer as the season progressed, by when most of the N had been depleted in the topsoil by leaching to the subsoil, where few roots had reached. Trudgill *et al.* (1975a) and Van Oijen *et al.* (1995) described specific effects of PCN on plant growth, such as reductions in light interception by accelerating leaf senescence, reductions in percentage ground cover, total leaf area, plant height and individual leaf area, and in some cases, lower plant nutrient status. Burstall and Harris (1983) showed a positive relationship between percentage ground cover and yield so any reduction in ground cover should adversely affect yield. One of the effects of stunting of roots is to reduce the volume of soil explored by the root system, which in turn reduces the root/soil interface and therefore potentially reduces nutrient and water uptake. Trudgill *et al.* (1975b) found reductions in the concentrations of N, P, K and Mg in plant dry matter but noted that only P and K were reduced on a fresh-weight basis. Fatemy and Evans (1986a) also showed that P, K and Mg uptake were reduced but Trudgill *et al.* (1975a) suggested that only chronic K deficiency resulted from PCN infestation. More recent work by de Ruijter (1998) supports previous findings that PCN induce or aggravate P deficiency. Evans, Parkinson & Trudgill (1975) also suggested that water stress was a yield limiting factor based on the greater stomatal resistances and more negative water potentials found in infected plants. Haverkort *et al.* (1994) agreed that the amount of water taken up is reduced but, unlike Evans (1982a), who suggested that water use efficiency, as measured by transpiration ratio, is also decreased, Haverkort *et al.* suggested that water use efficiency is not affected. Evans (1982c) also showed that where nematodes invade potatoes there is a higher risk of infection from the pathogen *Verticillium dahliae* and that this will increase the yield loss associated with PCN.

A further effect of nematode damage has been suggested by Davies (1995). Wound reactions in plants can activate the gene sequence of Pin2 mRNA (proteinase inhibitor II) which act on enzymes responsible for the hydrolysis of proteins. Pin2 mRNA is thought to be modulated by abscisic acid (ABA) or jasmonic acid (JA) when gene expression is induced at a distance from the actual wound site, which corresponds to Pin2 mRNA accumulation within the leaves but not in the roots of nematode infected plants (Yamagishi *et al.*, 1993). It is suggested that these gene expressions prevent plant processes which require large amounts of energy, e.g. those related to plant growth, and there are indications that in these circumstances processes such as the production of ribulose biphosphate carboxylase and the 10kd protein of the water splitting apparatus (both involved in photosynthesis) are prevented because gene expression is turned off. The activity of nitrate reductase can also be affected by proteinase inhibition as the actual rate of nitrate degradation is reduced (Salisbury and Ross, 1992). Such reactions may, therefore, be responsible for the reduced growth of potato plants infected with PCN. Evans (1982a) indicated that PCN do affect plant hormone production in that levels of ABA are increased in leaves, which could have been caused by water stress (Salisbury and Ross, 1992) also associated with PCN infection, and which triggers the production of ABA. Furthermore, cultivars intolerant of PCN attack may have greatly increased levels of ABA in their leaves when attacked by PCN whereas tolerant cultivars may not. Thus, if a tolerant cultivar shows lower increases in ABA production, then Pin2 will not be activated and growth will occur either normally or at only a slightly reduced rate. When PCN infestation is heavier and plants are more stressed, however, the Pin2 response could seriously reduce the growth of the plant.

1.4.5 Plant tolerance of invasion

Dale *et al.* (1988) define tolerant genotypes as different from intolerant genotypes in being able to produce greater yields under similar stressful growing conditions. Tolerance does not prevent PCN multiplication but normally gives the plant characteristics which allow it to grow well despite being invaded. Cook & Evans (1987) suggested that tolerance is not a type of resistance and used Jones & Kempton's (1978) definition of tolerance to describe the amount of host injury: a tolerant plant suffers little injury even when quite heavily infected whereas an intolerant plant suffers much injury. Reduction in root growth when an intolerant plant is invaded may indirectly reduce the nematode reproduction rate and therefore confer resistance; similarly, any reduced multiplication brought about by resistance may confer tolerance, and an interaction of the resistance and tolerance is possible. Evans and Haydock (1990), however, stress that resistance and tolerance are different attributes of a plant and point out that, although the two may interact, they should be considered as independent.

The measurement and subsequent definition of tolerance is perhaps best related to final crop yield as this is its most important consequence. Evans & Trudgill (1992) suggest that potato cultivars differ considerably in their tolerance of attack when tolerant cultivars are defined as those which suffer a smaller reduction in yield at high nematode densities. Variation in levels of tolerance has been demonstrated on several occasions. Evans (1982b) reported that reductions in yield ranged from 4.8 t/ha in the resistant cultivar Cara, to 32.9 t/ha in the susceptible cultivar Pentland Dell. In an earlier study, Evans & Franco (1979) noted a range of tolerance and quantified it by calculating a ratio of yields between infested and uninfested sites.

Trudgill (1986, 1987) carried out grafting experiments and demonstrated that tolerance was affected by both top and root factors. Further experiments by Trudgill and Phillips (1992), however, suggested that the root stock had the greater effect on conferring tolerance. These experiments utilised Cara (tolerant) and Pentland Dell (intolerant) to demonstrate the effects of rootstock and scion and showed that good top growth or extensive (strong) root growth can confer tolerance, or at least reduce the effects of PCN invasion. Trudgill *et al.* (1983) and Trudgill (1987) also demonstrated that, although yield is related to PCN population density, the relationship is also affected by the soil type. In peaty loams, where nutrient reserves would be high, PCN populations of 121 eggs/g soil reduced Pentland Dell yields by only 5% and Cara yields were not affected, whereas in sandy loams PCN populations of only 18 eggs/g soil reduced yields by 50% in Pentland Dell and 12% in Cara.

The deterministic nature of the potato cultivar is also important in relation to N use or requirement (Anon, 1993). The cultivars Cara, Maris Piper and Russett Burbank are indeterminate, whereas Estima, Wilja, Romano and Ausonia are relatively determinate. Their patterns of N use may confer tolerance in that the potentially lower N requirement of indeterminate cultivars could reduce the potential effect of reduced N uptake during PCN infestation. Therefore, as Cara and Maris Piper are tolerant of PCN invasion, and are also indeterminate cultivars, a link between the two traits may exist.

Tolerance identification and quantification was considered by Fatemy and Evans (1986b) in relation to the water uptakes and Ca concentrations of different potato cultivars. The findings indicated a highly significant correlation between water use and Ca concentration of the plant but even though the total water use in infected plants was reduced, the change in total Ca uptake was not greatly affected. There was also no correlation between the transpiration ratio and Ca concentration, probably because nematode infection makes roots more permeable to Ca (Price & Hague or Price, Clarkson & Hague).

Arntzen *et al.* (1993) found no correlation between tolerance and hatching ability of root diffusates collected from individual cultivars and, in later experiments (Arntzen *et al.*, 1994) measured rates of root growth of infected plants *in vitro* without finding any correlation between root growth and tolerance. Tolerance was, however, correlated with rate of hatching and growth of roots after inoculation.

1.4.6 Control of PCN

There are several options for the control of PCN: Granular nematicides, e.g. oxamyl (Vydate 10G) and aldicarb (Temik 10G), which are incorporated into the soil just prior to planting and which Trudgill (1986) suggests should prevent most of the yield loss associated with PCN infestations; soil fumigant-nematicides, e.g. 1,3-dichloropropene (Telone II) and Dazomet (Dazomet 98), injected into the soil in the autumn; crop rotation, which allows time for a natural decline of PCN levels; resistant cultivars, although at present we only have cultivars fully resistant to *G. rostochiensis* and cultivars partially resistant to *G. pallida*; trap cropping, by which PCN are stimulated to hatch and invade a sacrificial potato crop, which is removed from the field before new cysts develop, and which Whitehead *et al.* (1994) suggests is capable of reducing populations of 40-465 eggs/g by upwards of 75% in six weeks if carried out correctly; integrated pest management, which utilises all of the available control measures to give an economic return from the crop, and which Jones (1969) suggested could, in the form of a four year rotation with a resistant cultivar and the use of a nematicide, would achieve 99.9% control of *G. rostochiensis*; and finally legislative control, which is based on the Potato Cyst Eelworm (Great Britain) 1973 order, made as a direct result of the EC PCN directive of 1969 (69/465/EEC), whereby soil testing is used as the method of determining whether land is free from PCN and suitable for the growing of potato seed. Imported and exported plant material is also closely inspected for contamination with PCN to prevent their further spread, especially of pathotypes of the pest which may not be present in the country receiving the material.

The most important first step in any PCN control programme is determination of the infestation level in soil. The sampling strategy employed to attain a sufficiently reliable estimation of the infestation will depend on the end use of this information. Where accreditation is required in order to grow seed potatoes in 'PCN-free' land a more rigid technique is required than if the information is for use as a tool for management. In a review on sampling requirements, Haydock and Evans (1994) suggested that for routine sampling approximately 50 cores of 8 ml are required from each area for which a decision is required. ADAS classify infestations into the following categories : Low, 1 to 10 eggs/g; Moderate, 11 to 60 eggs/g; High, >60 eggs/g (Anon, 1986). Research carried out by Greco *et al.* (1982), in Italy, suggests that for *G. pallida* the crop tolerance level is only 1.7 eggs/g soil before yield loss begins, but that populations must reach 30 eggs/g soil before the symptoms of attack can be readily seen in the growing crop.

1.4.7 Combined PCN and fertiliser research

An early trial carried out by O'Brien & Prentice (1930) gave yield benefits from applying 20 t/acre of farmyard manure (FYM) to a sick potato crop over that from a quantity of artificial manure. The 'potato soil sickness' to which they referred, was attributed to the nematode pest *Heterodera schachtii* which, due to the later changes in nematology classification, would suggest the presence of PCN. The FYM application was described as being made through the drill at planting, but the methodology is unclear. No reduction in cyst content of the soil was found after the crop. No information is given, however, as to the type of FYM or soil nutrient levels. O'Brien & Prentice (1930) suggested, however, that the yield benefit was derived from a delay in root invasion until later in the season, but no discussion was made of the possible reasons for this delay. If the FYM contained large quantities of straw, from bedding, this may have led to better moisture retention within the soil and thus less water stress for the crop; alternatively, the FYM may have been of a more liquid type, which could have affected potato root diffusate concentration early in the season, so causing the delayed root invasion. These suggestions are of course, all purely speculative.

Trudgill (1980) attempted to alleviate the effects of reduced N, P and K uptake by plants infected by PCN by varying the levels of individual nutrients available to the plant whilst maintaining a constant supply of the other nutrients. In these pot tests, where no nematicide was used, doubling the standard N, P and K levels significantly increased haulm and root weight at 14 weeks after planting. When this experiment was repeated in the field a basal fertiliser was initially applied and then additional fertilisers were added as required. No significant increases were found in growth and yield from the use of additional fertilisers. The conclusions from these trials were that P and N were more likely than K to be deficient in nematode infested plants. Several points are, however, worthy of note from the field trial: 1) tripling the application of superphosphate increased the amount of available P in the potato ridge by only 3%; 2) where double the quantity of K was applied, the available K in the potato ridge rose by 41%, but the increase in uptake of K was only slight in nematode infested plants compared with that in plants grown in plots treated with a nematicide. The lack of an effect of P in the field has since been suggested by Trudgill (1987) to be due to rapid fixation of the applied P into a non-available form. Trudgill (1987) summarised the results from three field experiments in relation to fertiliser effects. Where additional fertiliser had been applied a greater increase in growth was seen in plants from plots not treated with nematicides than from those where nematicides had been used. In field experiment three, however, the yield of the cultivar Pentland Dell (non-resistant and intolerant) increased markedly when the fertiliser application rate was doubled from 75 kg N/ha, 75 kg P_2O_5/ha and 105 kg K_2O/ha to 150 kg N/ha, 150 kg P_2O_5/ha and 210 kg K_2O/ha at all rates of nematicide. The yield from the tolerant cultivar Cara only increased in non-nematicide treated plots.

Jones (1977) discussed plant resistance and fertiliser use with a wide range of pests and reported that where N was applied as ammonium sulphate to a PCN infested site it more than doubled the crop yield over that achieved with FYM, in contradiction to the effect seen by O'Brien & Prentice (1930). Applications of P and K increased the yields only slightly but it was noted that the site was already well supplied with these nutrients.

It is unfortunate that no soil indices are given for any of the above field experiments as this makes correlation of the responses with the total nutrients available to the plants, rather than simply quantities of fertilisers, impossible. A response to 'extra fertiliser' in one experiment would not necessarily mean there would be a similar response in another experiment where soil reserves differed.

Villagarcia and Franco (1984) studied the effects of varying rates of P on plants grown in pots in a glasshouse and infected by *Globodera pallida* pathotype P_4A (this pathotype would be classified as Pa2 by the Kort *et al.* (1977) scheme). The rates of superphosphate (20% P_2O_5) used were 0, 120 and 240 ppm and PCN were inoculated at 20 eggs/g soil. A significant increase in yield was obtained by applications of P to PCN inoculated plants over the yield achieved from PCN inoculated plants without P or from uninfected plants to which no P was applied. Nitrogen and K applications also increased yields, with a greater effect from N.

Raispere (1990) carried out several experiments on the nutrition of the plant in relation to the development of potato cyst nematodes. Nitrogen applied at six times the normal rate appeared to disturb the metabolism of the plant and almost completely inhibited nematode development in susceptible and tolerant plants. It was concluded that moderately stressed plants gave the best conditions for juvenile development and if N, P and Ca levels were increased the numbers of females produced were reduced. It should be noted, however, that this paper was translated from the Russian language and that the interpretations, especially in technical areas, sometimes gave two similar meanings which could not be absolutely defined.

In some of the most recent research, de Ruijter (1998) investigated the effects of soil compaction, soil pH and phosphorus fertilisation on crop growth of PCN infected plants. Applications of P fertilisers reduced or prevented PCN-induced P deficiency but it was suggested that the quantities applied would not be acceptable for commercial potato production (225 kg P/ha). Crop senescence was accelerated in association with reduced nutrient concentrations and tolerance of cultivars to PCN invasion was associated with the production of additional roots and large haulm.

1.4.8 Other nematode and fertiliser research

Martin-Prevel (1977) discussed very briefly the work carried out on pineapples in the Ivory Coast, where above ground growth is poorer and the crop N and K contents are lower as the severity of nematode attack increases. The crop receives all of its N and K from foliar applications. A suggestion is made that the lower mineral content of the plant is not only a nematode effect on nutrient absorption, but also that the plant roots must excrete N and K. The nematode species was not identified in the paper and no indication was given of the rates of fertiliser application, the soil nutrient status or the experimental procedures used.

Spiegel *et al.* (1982) studied the effects of both the quantity of K application and the source of N, either ammonium NH_4^+ or nitrate NO_3^-, on tomato (*Lycopersicon esculentum.* Mill.) plant growth when infected by the root-knot nematode *Meloidogyne javanica*. They showed that increased plant growth occurred when increasing rates of K were applied and that greater plant weights were obtained when the N source was NH_4^+. Comparison of the N, P and K concentrations in the infected and non-infected plants, across the range of K application rates, showed very little difference in K, a serious reduction in P concentration in the tops of infected plants, and very little difference in N concentrations. No discussion was made of the effects of the nematode on the much reduced P concentrations in the plant tops, which had decreased with increasing quantities of K application. This may well have influenced both the parasitism effects and the plant nutrition. The conclusions were that increased K nutrition of the plant appeared to increase the tolerance of the plant to infection by *Meloidogyne javanica* and that K accumulation in the roots was not due to interference in K transport upwards from the roots.

Prot *et al.* (1994) evaluated the use of increased N rate on rice to mitigate the growth and yield reductions associated with the root knot nematode *Meloidogyne graminicola.* Nitrogen applications increased the yields of both infected and non-infected plants but not, apparently, by specific amelioration of the effects of nematode infection.

1.5 Conclusions of the literature review

The potato cyst nematodes are serious pests of the potato crop, causing yield loss and thereby financial loss to growers. The potato crop does have a mechanism by which to withstand the damage caused by PCN, tolerance, but tolerance varies between cultivars and with environmental conditions, and is not sufficient alone to maintain the plant's ability to produce an economic yield at high levels of PCN infestation. The literature reviewed gives some indication that improving the nutrient availability to the plant may enhance its tolerance of attack from PCN but there is no definitive work to suggest which single nutrient or combination of nutrients are most limiting crop growth and yield. No work with PCN was found which had utilised foliar fertilisers. This method of fertiliser application is commonly used with micro-nutrients and the macro-nutrient N but less so for P and K. Application of nutrients via the foliage would by-pass the PCN damaged root system. In view of the high quantities of nutrients that need to be applied to potato crops, however, and the problems this brings for foliar fertilisers, investigations into the potential of the more efficient liquid placed fertilisers is also worthy of consideration.

1.6 Aims and objectives of the project

The broad aim of this research was to investigate the use of fertiliser applications to ameliorate the reduced nutrient uptake of PCN infected plants and thereby increase the plants yield and tolerance. These aims were to be met by investigations of whether :

a) foliar applied nutrients could by-pass the PCN damaged root system, redress the shortfall in plant nutrition and provide the nutrients limiting to plant growth.

b) foliar applications of N, P and K could identify whether any of these nutrients were severely restricting plant growth.

c) the use of foliar applied nutrients could increase the efficiency of fertiliser inputs to PCN infected plants.

d) liquid placed fertiliser was a more suitable and efficient method of basal fertiliser application to PCN infected plants.

The first year investigations were focussed on the following individual aims to provide a base from which the research could be built:

a) to determine if any of the fertiliser application methods affect the final crop yield, tuber number and size grading, crop growth, tolerance and nutrient concentrations within the plant.

b) to determine whether a set programme of foliar applications could adequately supply any limiting N, P and K requirements of the plant and show where a deficiency may exist.

c) to determine the response in items a and b (above) at recommended levels of nutrient application as a starting point for future work.

2. General materials and methods

The materials and methods described in this section have been separated from the experiments themselves as many are standard techniques in PCN research, used in the majority of the experiments and therefore common to most of them. Where changes of, or additions to, methodology or materials have been made between experiments, they are reported under the individual experiments.

2.1 Field and laboratory work

2.1.1 Treatment application of foliar nutrients

All foliar nutrient treatments were applied with a two-metre, one-man-operated, CO_2- powered AZO plot sprayer. The sprayer delivered 300 litres/ha at 200 Kpa , with Lurmark 03/F110 flat fan nozzles giving a medium quality spray (Anon, 1986). All applications were made after 5.00 pm on the days of application. In the foliar nutrients, N was supplied as Nufol (20% w/v urea N, Hydro-Agri (UK)), P as ortho-phosphoric acid (54% P_2O_5 w/w, Hydro-Agri (UK)), and K as potassium chloride (60% w/w K_2O, Hydro Agri (UK)).

2.1.2 PCN sampling and species determination

Initial sampling of the field experiment sites, to ascertain their suitability for PCN experiments, was carried out by dividing one ha sections of the field into 20m x 20m sampling areas. Each sampling area was then sampled by taking thirty cores (each 10cm x 1.5cm) in a W-pattern to form one bulked sample for the area. During the experiments, individual plots (which comprised three 1.83 m beds -equivalent to six rows at 91.5 cm spacings) were sampled to determine the initial (Pi) and final (Pf) population densities by taking a total of 60 cores from the two rows of the central bed and one row to either side of this bed. Pi samples were taken at the time of planting and Pf samples one day after harvest. A soil corer 10 cm long x 1.5 cm diameter was used for all PCN soil sampling. The samples were dried at 20-25°C for a minimum of 5 days in a heated continuous flow ventilated drying room, passed through a 4 mm sieve to remove stones, thoroughly mixed, and a 200g sub-sample taken. Cyst extraction and subsequent egg counts were carried out using procedures outlined by Shepherd (1986). Species determination was carried out using an isoelectric focusing technique based on that described by Fleming and Marks (1983) and Marks and Fleming (1985).

2.1.3 Emergence assessments

Plants were counted as emerged when any part of the plant shoot was visible when viewed from above the plant station. When all plant stations were emerged in a plot, that count provided a base from which all earlier emergence counts could be calculated as percentages (Bastiman, Bevis and Wellings, 1985).

2.1.4 Percentage ground cover

Percentage ground cover was estimated with the aid of a viewing frame which consisted of two 1.5m uprights strapped together with angle iron and also connected by two horizontal flat metal strips. The horizontal strips were located near the top of the uprights, 15 cm apart, and each contained 20 uniformly spaced four mm holes which were used to view the crop or ground (the holes in the two strips being in vertical alignment). The percentage ground cover was established by placing the frame over the central bed of each plot, at five stations, and the number of holes through which leaves could be seen was recorded for each station. When the total numbers of holes through which leaves could be seen at all five stations were added together they provided a percentage of ground covered for the plot (B J Legg & R J Parkinson, personal communication).

2.1.5 Leaf area index

In 1996 a viewing frame, as described by Korva & Forbes (1995), was used for the for non-destructive measurement of leaf area index. The viewing section, 0.9 m long and 30cm wide, contained 27 13mm viewing holes, spaced 10 cm apart. The grid size used for the viewing frame (10cm x 10cm) should, according to Korva and Forbes (1995), give a standard error of 10%. To bring the standard error down to 5% the grid cell size would have to be reduced to 5cm x 5cm but this would increase the time for one complete observation four-fold (four times the number of holes). The technique was validated by measuring 20 individual stations of crop with the viewing frame, from which the haulms were then removed and leaf area measured using a Delta T leaf area meter, mkII (Delta T Devices Ltd, Cambridge, UK). The difference between the two methods revealed a 5% higher value for the viewing table method but, as only the viewing table was used in the experiment, all of the results were similarly biased. In all other experiments the estimation of leaf area, and the subsequently calculated leaf area index, was achieved by removing whole plants from one or both rows to the side of the central potato bed in each plot. The leaves were then stripped from the plant and measured using the Delta T leaf area meter, mkII.

2.1.6 Timing of tuber initiation and first foliar nutrient applications

In the 1996 experiments, the first foliar nutrient applications were triggered when the accumulated air temperature, from planting, had reached 660 degree days (i.e. base = 0°C) which, according to Jefferies and Mackerron (1987), would be the start of tuber initiation for the cultivar Pentland Dell which was grown for these experiments. Establishment of tuber initiation time was achieved in the 1997 experiments by monitoring random plant samples in guard-only rows for the time when the tip of the stolon had swollen to twice its normal diameter on several stolons per plant (Jefferies and Lawson, 1991).

2.1.7 Plant sampling and root invasion

Whole plant samples were taken from experiments by removing one plant from each row at either side of the central potato bed in each plot (i.e. two plants per plot). A vertical slice was first cut down the ridge with a spade, mid-way between adjacent plants, then by gently working the soil around the plant with a fork the whole plant with roots was lifted out and placed in a large strong polythene bag. The soil was then forked over to remove any remaining roots which were then placed into the same polythene bag. Approximately 250 ml of water was added to each polythene bag to prevent wilting of the plant during transport to the laboratory. The plants were dissected into component parts (root, stolon, lower stem, above ground plant and tubers) which were weighed fresh and counted if appropriate, dried at 80°C for 48 hours and then re-weighed. A 2g, fresh weight, sub-sample of roots was taken from a mixture of the roots of the two plants from each plot. This sample was preserved in formal-acetic alcohol (FAA), which is a formaldehyde based preservative, to allow estimation of PCN root invasion to be made at a later date, as described by Hooper (1986a, 1986b).

2.1.8 Environmental monitoring

In 1998 rainfall and air temperature data was collected via an Adcon ET weather station (DMA Sales, Cambridge, UK), which gathered data every 30 minutes throughout the growing season.

i) Soil moisture deficits

All field experiments were normally monitored at seven day intervals for soil moisture deficits (SMDs) by using an Institute of Hydrology neutron probe (Wallingford, Oxon). Field capacity was established for each experimental site, after planting, by flooding the soil surrounding four neutron probe access points, designated for the purpose on the edge of the experiments. The calibration curve was then established for the site. Measurements for SMD were made through the season using access points within the experiment.

ii) Soil temperature

Gemini soil temperature dataloggers, Tinytalk® II (Chichester, West Sussex, UK), were installed at 20 cm depth in the centre of a potato ridge (replacing a planted seed tuber) in a guard row within the experiments, and set to read at 2.5 hr intervals.

iii) Air temperature

In 1996 and 1997 air temperatures were recorded with Gemini temperature dataloggers, Tinytag® (Chichester, West Sussex, UK). The dataloggers were situated within the experiments, at a height of 1.5 m, within a white, ventilated sun shelter. Temperatures were logged at 2.5 hr intervals throughout the experiment.

iv) Precipitation

In 1996 and 1997 precipitation was recorded with a Rain-o-matic® raingauge (ELE International, Hemel Hempstead, UK). The raingauge was situated in the centre of the experiments, at a height of 1.5 m. Measurements were taken throughout the experimental period for comparison with the SMD measurements and to give a total figure for precipitation.

2.1.9 Leaf samples

Twenty leaves per plot (youngest fully mature leaf, 4th from the top of the plant) were removed from plants at several times during the growth of the crop to provide material for measurement of plant nutrient status. The samples were taken in the early morning and placed in brown paper bags which were kept in a 'cool' box (approx 5 °C) for transport to the laboratory. In the laboratory, the leaves were washed in a 0.1% solution of 'Teepol' for 30 seconds to remove dirt and agrochemical contaminants and then rinsed twice in deionised water for 20 seconds each time. The samples were then oven dried at 75 °C for 36 hrs and stored in cool dry conditions (Reuter, Robinson, Peverill & Price, 1986).

2.1.10 Chlorophyll readings

In 1997 the quantity of chlorophyll present in the youngest fully mature leaf was measured with a Minolta Spad 502 hand held chlorophyll meter as described by Vos and Bom (1993). These measurements were taken at 66, 84, 98, 112, 119 and 133 days after planting. The instrument measures chlorophyll content by measuring the transmittance of a leaf at approximately 430 and 750 nm. Thirty observations were made in each plot.

2.1.11 Nutrient analysis of plant material

Whole plant or fourth leaf samples were collected, decontaminated and dried as described in section vii and ix. The samples were milled to pass a 1mm screen with a Cyclotec mill 1093 sample mill (Tecator, Reading, UK). Each sample was then thoroughly mixed. Subsamples (1g for %N and 2.5g for %P and %K determination) were taken, oven dried overnight at 60°C and re-weighed before further preparation. Nitrogen content was determined titrimetrically using analysis for total nitrogen by the semi-automated Kjeldahl method (Bailey, 1986; Helrich, 1990). Samples for P and K determination were ashed overnight at 500°C in a Gallenkamp muffle furnace. Ashed samples were then prepared and analysed for nutrient content. Total phosphorus content was determined by spectrophotometric determination of the phospho-vanado-molybdate complex (Bailey, 1986; Helrich 1990), at a wavelength of 400 nm using a Beckman DU 640 spectrophotometer (Beckman Instruments, California, USA). Total K was determined by flame emission spectrophotometry (Bailey, 1986; Helrich, 1990) using a Smith-Hieftje 1000 atomic absorption spectrophotometer (Thermo-Jarrell Ash Corporation, Franklyn, MA, USA) at a wavelength of 766.5 nm.

2.1.12 Leaf discolouration

In 1997 a leaf discolouration was seen at 91 days after planting (DAP) in the form of 'brown speckling'. By 98 DAP these individual brown speckles had coalesced to form larger discoloured areas on the leaves. The following scoring system was devised to quantify the levels of discolouration seen in the central five metres of the yield beds and was based on a maximum of 30 plant stations per five metres of bed :

0.0	No effects seen.
0.1	A few scattered leaves showing leaf discolouration.
1.0	The majority of plants showing slight leaf discolouration.
5.0	The majority of plants showing slight leaf discolouration plus 1-10 plants showing coalesced discolouration.
7.5	The majority of plants showing slight leaf discolouration plus 10-20 plants showing coalesced discolouration.
10	Majority of plants showing coalesced leaf discolouration.
15	Majority of plants showing coalesced leaf discolouration plus slight leaf necrosis.
20	Majority of plants showing coalesced leaf discolouration plus 1-10 plants showing leaf necrosis.
50	Majority of plants showing coalesced leaf discolouration plus 10-20 plants showing leaf necrosis.
75	Majority of plants showing coalesced leaf discolouration and all plant leaves necrotic.
100	All leaves discoloured, necrotic and leaf loss occurring.

Note : this assessment was carried out visually without the aid of equipment.

2.1.13 Harvest

The 1996 field experiments were harvested by hand two weeks after desiccation with sulphuric acid. The 1997 experiment was allowed to senesce naturally and the 1998 experiment was desiccated with glufosinate-ammonium as Harvest (150 g/litre glufosinate-ammonium SL, Agrevo (UK)). The 1997 and 1998 experiments were both harvested by first removing the potatoes from the plot ends by hand and then using a tractor mounted 'Massey Ferguson' single row potato spinner to harvest the main plot area, followed by hand forking. Plot yields in all field experiments were taken from six metres of the central bed, giving a harvest area of $10.98m^2$. The tubers were graded over a 'Cooke' grader line, splitting the grades into <40 mm, 40-60 mm, 60-80 mm and >80 mm fractions, by weight and number. Dry matter was measured, during grading, with a hydrometer (Zeal, London, England), one day after harvest.

2.2 Statistical analysis and data handling

The data produced by assessments was analysed with Genstat™ for Windows version 3.2. (Lawes Agricultural Trust, IACR-Rothamsted, UK). Analytical procedures included analysis of variance, analysis of variance with additional control, analysis of variance for split-plot experiments, planned orthogonal contrasts of interest, rate response of orthogonal polynomials, regression and blocked experiment regression analysis (Pearce *et al.*, 1988; Pearce, 1992a and 1992b; Mead, Curnow & Hasted, 1993) and when appropriate with covariates (Gomez & Gomez, 1984). Data were analysed untransformed wherever possible but, where data showed a skewed distribution, or would be more accurately represented (i.e. where percentages were estimated) by transformed values, the appropriate transformation of data was carried out before analysis (Gomez & Gomez, 1984).

3. The 1996 field experiments

3.1 Introduction

Although an acknowledged mechanism of potato yield loss attributed to PCN infection is the reduced uptake of N, P and K (Trudgill *et al.*, 1975a, 1975b, 1975c), the literature on this subject is inconclusive. The literature reports no experiments which have investigated foliar fertiliser application or basal fertiliser application methods in relation to PCN infection. The initial problems for this research were therefore four-fold: 1) would the basal fertiliser application method affect the tolerance of the plants ? 2) would the basal fertiliser method affect the plant response to foliar nutrient applications ? 3) which single nutrient or combination of nutrients was most limiting crop yields and was therefore required to ameliorate the nutrient deficiencies ? and 4) would the foliar nutrients need to be applied only once or at intervals throughout the season. The first experiments were therefore designed to investigate I) whether basal fertiliser application method could influence the tolerance of the plant or the response to foliar applications of N, P and K, and ii) whether a single application or combined applications of foliar N, P and K, in addition to a flat rate liquid placed fertiliser, could influence the tolerance of PCN infected plants in a set programme of applications. In both experiments a five spray programme was chosen to provide the plant with nutrients over the peak bulking period, to mimic to some degree the normal pattern of nutrient uptake, and to ensure that the lowest possible concentration of nutrients was used in the sprays in order to reduce the potential for leaf scorch. The quantities of foliar nutrients applied were based on the range of plant nutrient deficits noted from published experimental results. The cultivar Pentland Dell was chosen for the experiments based on its characteristics of no PCN resistance and a low level of PCN tolerance (Evans & Franco, 1979; Trudgill & Cotes, 1983; Trudgill, 1987). Nematicide and non-nematicide treatments were included in a split-plot design to give indications of tolerance with all treatments (Dale & Brown, 1989). It was felt that any differences which occurred as a result of the initial experiments would provide information on which further experimentation could be based.

3.1.1 Aims and objectives

i) Experiment one

The aims of this experiment were to investigate whether:

a) the basal fertiliser application method could influence the N, P and K concentration in tissues, the tolerance, and therefore the yield of PCN infected potatoes.

b) applications of foliar N, P and K were affected by the basal fertiliser application method.

The title for this experiment was:

The effects of fertiliser application type and foliar NPK on the growth and yield of potatoes infected by the potato cyst nematode *Globodera pallida*.

ii) Experiment two

The aims of this experiment were to investigate whether:

a) individual or combined applications of foliar N, P and K could improve the nutrient concentrations, growth, yield and tolerance of PCN infected plants.

b) the programme of foliar N, P and K applications was a suitable method of ameliorating the nutrient deficiencies associated with PCN infection.

c) foliar applications of N, P and K highlighted any deficiencies of these three elements associated with PCN infection.

d) foliar applications of N, P and K influenced plant invasion by or population development of PCN.

The title for this experiment was:

The effects of individual and combined applications of foliar NPK on the growth and yield of potatoes infected by the potato cyst nematode, *Globodera pallida*.

3.2 General materials and methods

The field experiment, situated near Newport, Shropshire, UK, grid reference SJ785156 was a Newport series sandy loam (O.S., 1983) with ADAS (Anon, 1994) nutrient indices of : N 0.0; P 5.0 (73 mg P/l); K 3.1 (257 mg K/l); Mg 2.9 (96 mg Mg/l), and pH 7.2. The experimental design was a split-plot randomised complete block with five replicates. Each whole plot was 8 m long and 11 m wide (i.e. with twelve rows). Whole plots were split into two six row sub-plots, one sub-plot receiving no nematicide and the other receiving the nematicide oxamyl at 5.5 kg a.i./ha as Vydate 10G (10% oxamyl w/w gr.; Du Pont (UK) Ltd). The nematicide was applied onto pre-formed beds with a gravity microband applicator (Horstine Farmery Equipment) mounted on a bed-tiller/bed-former (Dowdswell, UK) which incorporated the nematicide to approximately 35 cm depth (Woods, 1997). The potatoes, cv. Pentland Dell (Super Elite grade II graded to 30-40 mm) were planted un-sprouted on the 27th April at 20 cm depth and 30 cm in-row spacing; rows were 91.5 cm wide. Irrigation was applied using a centre pivot irrigation system to maintain a season mean soil moisture deficit of 25 mm The crop was grown using standard agrochemical practices for the control of weeds and the disease 'late blight' (*Phytophthora infestans*) in a commercial potato crop.

3.2.1 Specific to experiment one

The effects of fertiliser application type and foliar NPK on the growth and yield of potatoes infected by the potato cyst nematode, *Globodera pallida*.

Treatment fertiliser applications (Table 3.1) were: granular fertilisers broadcast by hand onto formed beds prior to bed tilling and liquid placed fertilisers applied at planting with a planter mounted Chafer liquid fertiliser injection system on the day of planting. Granular fertilisers were sourced as urea (46% N), triple superphosphate (43% P_2O_5 soluble in water), muriate of potash (60% K_2O soluble in water). Liquid placed fertilisers were applied in two bands at 5 cm below and 5 cm to the side of the seed tubers. A high rate of liquid fertiliser (1263 l/ha) was calibrated and applied through the Chafer system whilst the lower rate (1200 l/ha) was calibrated through a modified Azo sprayer system and applied through a separate set of injection nozzles welded to the Chafer system (Plate 3.1). The liquid fertilisers used for the high rate (LF in Table 3.1) were Hydro-Chafer 8.4.12 and 11.11.11, mixed on a 1:1 ratio and applied at 1263 l/ha to give 120 kg N/ha, 100 kg P_2O_5/ha and 150 kg K_2O/ha. The liquid fertiliser used for the low rate (LF + F in Table 3.1) were a combination of Hydro-Chafer 8.4.12 (94 litres) + 11.11.11 (80 litres) + Nufol N20 (43.5 litres) + water (32.5 litres) mixed together to give a final NPK ratio of 10.5.8 which, when applied at 1200 l/ha, gave 120 kg N/ha, 60 kg P_2O_5/ha and 96 kg K_2O/ha. An application of 120 kg N/ha as urea (46% N) was made to all plots receiving fertiliser at tuber initiation. The foliar applications were made only after 5.00 pm at an average of every 10 days starting on 20th June. The first application was triggered when the accumulated air temperature, from planting, had reached 660 degree days (above a 0°C base). Subsequent observation showed that the first foliar application actually occurred 5 days prior to tuber initiation or 54 days after planting (DAP). Foliar NPK applications were made up of Hydro-Chafer 11.11.11 (35.46 litres) + 20.0.10 (10.50 litres) + Water (104.04 litres), giving a fertiliser ratio of 4:2.6:3.3. All foliar applications delivered 12 kg N/ha, 7.8 kg P_2O_5/ha and 9.9 K_2O/ha. A 10.98 m^2 area of each plot was harvested using a Grimme Colt 88 destoner followed by forking through on the 2nd October 1996 (158 DAP). All tubers found were collected by hand into 25kg bags which were then removed from the field, weighed and graded. The mean initial PCN population density, identified as *G. pallida*, was 19 eggs/g soil.

Plate 3.1. Modified Hydro-Chafer liquid fertiliser placement equipment, mounted on a Faun automatic potato planter, showing modified Azo sprayer, used for liquid fertiliser application at Lynn South, Shropshire.

Table 3.1. Fertiliser treatments in an investigation of the effects of fertiliser application type and foliar NPK on the growth and yield of potatoes infected by *Globodera pallida*.

	Fertiliser application (kg/ha)						
treatment	at planting			at TI [b]	five individual foliar (total)		
code [a]	N	P_2O_5	K_2O	N	N	P_2O_5	K_2O
NF	0	0	0	0	0	0	0
BF	120	100	150	120	0	0	0
BF+F	120	60	100	60	12(60)	8(40)	10(50)
LF	120	100	150	120	0	0	0
LF+F	120	60	100	60	12(60)	8(40)	10(50)

[a] NF = No fertiliser, BF = broadcast fertiliser only, BF+F = broadcast fertiliser + foliar, LF = liquid fertiliser, LF+F = liquid fertiliser + foliar,
[b] TI = tuber initiation.

3.2.2 Specific to experiment two

The effects of individual and combined applications of foliar NPK on the growth and yield of potatoes infected by the potato cyst nematode, *Globodera pallida*.

Basal liquid fertiliser, applied with a planter mounted Chafer liquid fertiliser injection system, was applied uniformly across the experiment at 1263 l/ha to give 120 kg N/ha, 100 kg P_2O_5/ha and 150 kg K_2O/ha. This was derived from Hydro-Agri 8.4.12 and 11.11.11 liquid fertilisers ((Hydro Agri (UK)) mixed on a 1:1 ratio. An application of 120 kg N/ha as ammonium nitrate (34% N, Hydro Extran) was broadcast on 12th July (76 DAP) across the whole experiment using a 24m Amozone fertiliser spreader. Foliar nutrient treatment applications (Table 3.2) consisted of five-spray programmes with individual treatments as follows: FW, water at 300 l/ha; Fol N, 300 l/ha 4% w/v urea N in water; Fol P, 300 l/ha 1.7% w/v Phosphoric acid in water; Fol K, 300 l/ha 2.5% w/v KCl; Fol NP, 300 l/ha 4% N and 1.7% P_2O_5 derived from Hydro-Chafer 20-10-0 and urea in water; Fol NK, 300 l/ha 4% w/v urea N and 2.5% w/v KCl in water; Fol PK, 300 l/ha 1.7% P_2O_5 and 2.5% K_2O derived from KCl and di-potassium hydrogen orthophosphate (anhydrous) in water; Fol NPK, 300 l/ha 4% N + 1.7% P_2O_5 + 2.5% K_2O derived from Nufol (20% w/v urea N), Hydro Chafer 20-0-10 and Hydro Chafer 11-11-11, in water (Table 3.2). Where nutrient applications were made, total applications of each nutrient were 12 kg N/ha, 5.1 kg P_2O_5/ha and 7.5 K_2O/ha. The foliar applications were made only after 5.00 pm at an average of every 13.5 days starting on 22nd June. The first application was triggered when the accumulated air temperature, from planting, had reached 660 degree days (i.e. base = 0°C). However, subsequent observation showed that the first foliar application actually occurred 3 days before tuber initiation or 56 DAP. Plots were harvested by hand on the 24th September 1996 (150 DAP), taking 10.98m^2 from the central bed of each plot. All tubers found were collected into 25kg sacks and removed from the field, weighed and graded. The mean initial PCN population density, identified as *G. pallida*, was 13 eggs/g soil.

Table 3.2. Foliar nutrient treatments in an investigation of the growth and yield response of potatoes infected by *Globodera pallida* to individual or combined applications of foliar N, P and K.

Treatment code	Foliar applications (%N)	(%P_2O_5)	(%K_2O)	Spray schedule, days after planting
Std + FW [a]	0.0	0.0	0.0	56, 73, 86, 102, 110
Std + Fol N	4.0	0.0	0.0	56, 73, 86, 102, 110
Std + Fol P	0.0	1.7	0.0	56, 73, 86, 102, 110
Std + Fol K	0.0	0.0	2.5	56, 73, 86, 102, 110
Std + Fol NP	4.0	1.7	0.0	56, 73, 86, 102, 110
Std + Fol NK	4.0	0.0	2.5	56, 73, 86, 102, 110
Std + Fol PK	0.0	1.7	2.5	56, 73, 86, 102, 110
Std + Fol NPK	4.0	1.7	2.5	56, 73, 86, 102, 110

[a] Std = standard seed-bed fertiliser only (240 kg N/ha; 100 kg P_2O_5/ha; 150 kg K_2O/ha), + FW = foliar water, + Fol N = foliar nitrogen, + Fol P = foliar phosphate, + Fol K = foliar potassium.

3.3 Results of experiment one

The effects of fertiliser application type and foliar NPK on the growth and yield of potatoes infected by the potato cyst nematode, *Globodera pallida*.

3.3.1 PCN populations

The PCN population in the experimental area was identified by isoelectric focusing as *G. pallida* with no indication of the presence of *G. rostochiensis*.

i) Initial population density

The initial PCN population densities (Pi, eggs/g soil) did not differ significantly between the experimental treatments (Table 3.3), so no individual treatment was under significantly higher or lower PCN pressure than any other. The mean PCN population density was 19 eggs/g soil. The C.V. of 38.6%, however, suggests that there was substantial variation across the experimental area.

ii) Final population density

The final PCN population densities (Pf, eggs/g soil) did not differ significantly between fertiliser treatments, or nematicide treatments, or show any significant treatment interactions (Table 3.3). The mean Pf of all plots treated with full rate oxamyl, 220 eggs/g soil, was not significantly different to the Pf of plots not treated with oxamyl, 210 eggs/g soil, demonstrating no retardation of PCN population development from oxamyl application.

iii) Pf/Pi ratios

The multiplication rates of PCN, as Pf/Pi ratios $\log_e$ transformed to achieve a normal distribution of data for analysis of variance, were not significantly affected by the addition of fertiliser to the soil as either broadcast granular or liquid placement methods. Nor did the application of oxamyl to plots reduce the multiplication rate of PCN (Table 3.4).

3.3.2 Potato root invasion by PCN

The number of PCN juveniles, all stages, counted in the stained potato roots, showed no significant effects of fertiliser type or application method. There was evidence ($P = 0.003$) to suggest that oxamyl application had prevented PCN root invasion to some degree, with a back-transformed mean of 376 juveniles/g root in plants from oxamyl treated plots compared with a mean of 672 juveniles/g root found in plants from plots not treated with oxamyl. The highest recorded invasion level of 1043 juveniles/g root occurred in plants from plots which had received neither fertiliser nor oxamyl. This invasion count, however, was not significantly higher than any other treatment even with a low coefficient of variation of counts (CV = 9.6 %) (Table 3.4).

Table 3.3. The initial (Pi) and final (Pf) PCN population densities in an investigation of the effects of fertiliser application type, foliar NPK and nematicide on the growth and yield of potatoes infected by PCN.

fertiliser method	Pi (eggs/g soil) without oxamyl	Pi (eggs/g soil) with oxamyl	Pi (eggs/g soil) method means	Pf (eggs/g soil) without oxamyl	Pf (eggs/g soil) with oxamyl	Pf (eggs/g soil) method means
NF [a]	18	19	19	234	227	231
BF	19	18	19	221	178	200
BF+F	26	22	24	240	262	251
LF	19	17	18	198	226	212
LF+F	13	15	14	157	204	180
oxamyl means	19	18		210	220	

Pi	SED	significance (P =)	d.f.	CV%
oxamyl means	2.0	n.s.	20	
method means	5.6	n.s.	16	
oxamyl*method	6.5	n.s.	26	38.6
oxamyl*method# [b]	4.5			
Pf				
oxamyl means	21.2	n.s.	20	
method means	44.0	n.s.	16	
oxamyl*method	31.52	n.s.	32	35.0
oxamyl*method#	47.5			

[a] see Table 3.1.

[b] (# when comparing within the same fertiliser method)

Table 3.4. The effects of fertiliser application type, foliar NPK and nematicide on the PCN population ratios (Pf/Pi) and root invasion (at 69 DAP) of potatoes infected by *Globodera pallida.*

	Log_e Pf/Pi (back-transformed)[b]			root invasion (juveniles/g root) Log_e (back-transformed)		
fertiliser method	without oxamyl	with oxamyl	method means	without oxamyl	with oxamyl	method means
NF [a]	2.54 (13)	2.69 (15)	2.62 (14)	6.95 (1043)	5.65 (284)	6.30 (545)
BF	2.82 (17)	2.35 (11)	2.59 (13)	6.36 (578)	5.80 (330)	6.08 (437)
BF+F	2.29 (10)	2.44 (12)	2.36 (11)	6.63 (757)	6.25 (518)	6.44 (626)
LF	2.71 (15)	2.74 (16)	2.72 (15)	6.23 (508)	5.73 (308)	5.98 (395)
LF+F	2.69 (15)	2.57 (13)	2.65 (14)	6.38 (590)	6.20 (493)	6.29 (539)
oxamyl means	2.61 (14)	2.57 (13)		6.51 (672)	5.93 (376)	

<u>Pf/Pi</u>	SED	significance (P =)	d.f.	CV %
oxamyl means	0.169	n.s.	20	
method means	0.377	n.s.	16	
oxamyl*method	0.463	n.s.	30	23.1
oxamyl*method# [c]	0.379			
<u>root invasion</u>				
oxamyl means	0.170	0.003	20	
method means	0.342	n.s.	16	
oxamyl*method	0.434	n.s.	32	9.6
oxamyl*method#	0.379			

[a] see Table 3.1.

[b] values in brackets are back-transformed means after analysis of variance.

[c] (# when comparing within the same fertiliser method)

3.3.3 Plant growth

i) Emergence

Neither the application of fertiliser nor the method of fertiliser application significantly affected the rate of plant emergence, however, oxamyl application significantly ($P = 0.013$) increased the rate of plant emergence at 40 DAP, irrespective of fertiliser application method (Table 3.5).

Table 3.5. The effects of fertiliser application type, foliar NPK and nematicide on the percentage emergence of potatoes, at 40 DAP, when infected by *Globodera pallida*.

Fertiliser method	without oxamyl	with oxamyl	method means
NF [a]	29.4	29.8	29.6
BF	27.8	30.0	28.9
BF+F	27.2	28.2	27.7
LF	28.4	29.0	28.7
LF+F	25.0	28.6	26.8
oxamyl means	27.56	29.12	

emergence	SED	significance (P =)	d.f.	CV %
oxamyl means	0.57	0.013	20	
method means	1.72	n.s.	16	
oxamyl*method	1.94	n.s.	25	7.1
oxamyl*method#	1.27			

(# when comparing within the same fertiliser method)

[a] see Table 3.1.

ii) Percentage ground cover

a) 61 DAP

The percentage ground cover, estimated at 7 days after the first foliar nutrient applications, showed no significant benefits from fertiliser application or between fertiliser application methods. Treating plots with oxamyl gave consistent ground cover benefits to all fertiliser applications and methods, and the mean percentage ground cover over fertiliser treatments was significantly ($P < 0.001$) increased by oxamyl application (Table 3.6).

b) 102 DAP

The values for percentage ground cover at 102 DAP had a highly skewed distribution which required arcsine transformation to give data suitable for analysis. The resulting transformed data was, however, still skewed to a degree and the significance of the results (Table 3.6) should be treated with some caution.

Plots which had received no fertiliser achieved significantly less ($P = 0.006$) percentage ground cover than plots receiving any type of fertiliser application, but there were no differences within fertiliser application methods. In plots not treated with oxamyl the liquid placed fertiliser plus foliar NPK produced the highest percentage ground cover (84.1%) which compared favourably with that estimated for plots with the same fertiliser application but which had been treated with oxamyl. Treating plots with oxamyl gave significant ($P = 0.012$) overall benefits to ground cover (Table 3.6).

<u>iii) Plant fresh-weight</u>

Seedbed and foliar fertiliser application did not significantly affect whole plant, above- ground biomass, root or tuber fresh-weights. Treating plots with oxamyl, however, showed significant benefits to whole-plant ($P = 0.008$), above-ground biomass ($P = 0.018$) and tuber ($P = 0.002$) fresh-weights. This benefit was seen, in all but one case, irrespective of the fertiliser application method. Where foliar NPK applications had replaced some of the seedbed application, the whole-plant, above ground biomass and root fresh-weights were all higher than where the whole quantity of fertiliser was applied in the seedbed, but not significantly (Table 3.7a & 3.7b).

Table 3.6. The effects of fertiliser application type, foliar NPK and nematicide on the percentage ground cover of potatoes, at 61 and 102 DAP, infected by *Globodera pallida*.

fertiliser method	61 DAP without oxamyl	61 DAP with oxamyl	61 DAP method means	102 DAP (arcsine transformed) without oxamyl	102 DAP (arcsine transformed) with oxamyl	102 DAP (arcsine transformed) method means
NF [a]	43.6	47.4	45.5	60.0	70.7	65.3
BF	49.2	52.4	50.8	76.3	78.2	77.2
BF+F	47.0	53.8	50.4	73.9	84.6	79.3
LF	51.4	54.4	52.9	78.2	87.4	82.8
LF+F	47.2	54.2	50.7	84.1	86.1	85.1
oxamyl means	47.7	52.4		74.5	81.4	

<u>61 DAP</u>	SED	significance (P =)	d.f.	CV %
oxamyl means	1.20	<0.001	20	
method means	2.51	n.s.	16	
oxamyl*method	3.15	n.s.	34	8.5
oxamyl*method# [b]	2.69			
<u>102 DAP</u>				
oxamyl means	2.52	0.012	20	
method means	4.64	0.006	16	
oxamyl*method	6.11	n.s.	34	11.4
oxamyl*method#	5.63			

[a] see Table 1.

[b] (# when comparing within the same fertiliser method)

Table 3.7a Plant fresh-weight (g) at 69 DAP in an investigation of the growth and yield response to nematicide and seedbed, tuber initiation and supplementary foliar nitrogen, of potatoes infected by *Globodera pallida.*

fertiliser method	whole plant wt (g)			above ground wt(g)		
	without oxamyl	with oxamyl	method means	without oxamyl	with oxamyl	method means
NF [a]	389.3	477.5	433.4	285.0	373.8	329.4
BF	415.6	495.2	455.4	331.6	386.8	359.2
BF+F	453.4	547.8	500.6	356.6	417.6	387.1
LF	461.6	578.0	519.8	368.4	436.6	402.5
LF+F	471.6	518.8	495.2	377.6	405.3	391.5
oxamyl means	438.3	523.5		343.8	404.0	

whole plant	SED	significance (P =)	d.f.	CV %
oxamyl means	29.15	0.008	20	
method means	59.9	n.s.	16	
oxamyl*method	75.60	n.s.	32	21.4
oxamyl*method# [b]	65.17			
above ground				
oxamyl means	23.28	0.018	20	
method means	48.14	n.s.	16	
oxamyl*method	60.60	n.s.	32	22.0
oxamyl*method#	52.06			

[a] see Table 1.

[b] (# when comparing within the same fertiliser method)

Table 3.7b Plant fresh-weight (g) at 69 DAP in an investigation of the growth and yield response to nematicide and seedbed, tuber initiation and supplementary foliar nitrogen, of potatoes infected by *Globodera pallida.*

fertiliser method	root wt (g) without oxamyl	root wt (g) with oxamyl	root wt (g) method means	tuber wt (g) without oxamyl	tuber wt (g) with oxamyl	tuber wt (g) method means
NF [a]	14.31	14.76	14.53	57.26	56.20	56.73
BF	13.09	14.17	13.63	39.72	59.30	49.51
BF+F	15.99	16.25	16.12	43.81	76.67	60.24
LF	11.67	13.20	12.43	51.29	90.34	70.81
LF+F	12.59	11.12	11.85	46.43	70.01	58.22
oxamyl means	13.53	13.90		47.70	70.50	

root wt	SED	significance (P =)	d.f.	CV %
oxamyl means	0.795	n.s.	20	
method means	2.112	n.s.	16	
oxamyl*method	2.458	n.s.	27	20.5
oxamyl*method# [b]	1.777			
tuber wt				
oxamyl means	6.326	0.002	20	
method means	9.028	n.s.	16	
oxamyl*method	13.474	n.s.	36	37.8
oxamyl*method#	14.145			

[a] see Table 1.

[b] (# when comparing within the same fertiliser method)

3.3.4 Plant nutrient status

i) Percentage N

There were no overall differences in N concentration between plots treated with oxamyl and those not treated with oxamyl. The concentration of N was significantly higher ($P = 0.013$)

in plants from all plots receiving fertiliser applications than from plots receiving no fertiliser, irrespective of the application method. In plots not treated with oxamyl, applying all of the fertiliser in the seedbed as placed liquid fertiliser resulted in a significantly higher ($P < 0.001$) N concentration in the plants than when the fertiliser was applied as a broadcast granular. When the fertiliser quantity was split between seedbed and foliar applications, significantly higher N concentrations ($P < 0.001$) were found when foliar applications were combined with placed liquid fertiliser, whereas foliar fertiliser combined with broadcast granular fertiliser failed to produce a significant change in N concentration (Table 3.8). In plots not treated with oxamyl, only the application of foliar fertiliser plus placed liquid fertiliser gave an equivalent or higher N concentration than its parallel treatment in plots treated with oxamyl.

ii) Percentage P

There were no significant differences in the whole-plant concentration of P between any of the treatment. Placed liquid fertiliser increased the P concentration within plants to a level almost significantly (P =0.053) greater than found where broadcast granular fertilisers were used, irrespective of oxamyl application. When the fertiliser quantity was split between seedbed and foliar applications, P concentration was higher in plants where no oxamyl was applied than in plants where oxamyl had been applied (Table 3.8).

iii) Percentage K

The application of oxamyl did not significantly affect the K concentration within plants. Where fertilisers were applied as liquid placed or liquid placed plus foliar NPK the K concentrations were significantly (P =0.001) greater than those achieved with broadcast granular fertiliser with or without foliar NPK applications. In plots not treated with oxamyl only the use of liquid placed fertiliser plus foliar NPK gave concentrations of K similar to or higher than those found in plants from plots treated with oxamyl (Table 3.8).

Table 3.8. The effects of fertiliser application type, foliar NPK and nematicide on the nutrient status of whole potato plants infected by *Globodera pallida* measured 69 DAP (four days after the second foliar application).

fertiliser method	% N in d.m.			% P in d.m.			% K in d.m.		
	- O [a]	+ O	method mean	- O	+ O	method mean	- O	+ O	method mean
NF [b]	2.99	3.27	3.13	0.274	0.333	0.304	3.80	4.38	4.09
BF	3.43	3.53	3.48	0.295	0.317	0.306	4.21	4.52	4.36
BF+F	3.43	3.45	3.44	0.314	0.300	0.307	4.40	4.46	4.43
LF	3.65	3.75	3.70	0.363	0.361	0.362	4.90	5.09	5.00
LF+F	3.80	3.45	3.62	0.382	0.327	0.355	5.10	4.91	5.01
oxamyl means	3.46	3.49		0.326	0.327		4.48	4.67	

<u>% N in d.m.</u>	SED	significance (*P* =)	d.f.	CV %
oxamyl means	0.051	n.s.	20	
method means	0.089	<0.001	16	
oxamyl*method	0.120	0.013	35	5.2
oxamyl*method# [c]	0.115			
<u>% P in d.m.</u>				
oxamyl means	0.0119	n.s.	20	
method means	0.0239	n.s. (0.053)	16	
oxamyl*method	0.0304	n.s.	32	12.9
oxamyl*method#	0.0266			
<u>% K in d.m.</u>				
oxamyl means	0.112	n.s.	20	
method means	0.208	0.001	16	
oxamyl*method	0.273	n.s.	34	8.7
oxamyl*method#	0.251			

[a] - O = without oxamyl, + O = with oxamyl.
[b] see Table 3.1.
[c] (# when comparing within the same fertiliser method)

3.3.5 Tuber yield

There were no significant effects on tuber yield of oxamyl or fertiliser application type in any of the tuber grades measured (< 40mm, 40-60mm and total yield) but oxamyl application did give weak evidence ($P = 0.056$) of an overall yield benefit in the 40-60mm grade. The highest yields in plots not treated with oxamyl came from fertiliser applications based on liquid placed fertiliser; these were, however, only slightly higher than those achieved with broadcast granular fertilisers. The highest yield was achieved where the fertiliser was split between liquid placed seedbed fertiliser and foliar NPK application in oxamyl treated plots (37.2 t/ha). The lowest yield of 24.9 t/ha was from plots where no oxamyl or fertilisers were applied (Table 3.9).

i) Tuber number

There were no significant fertiliser effects on the number of tubers in the <40mm, 40-60mm or the total number of tubers produced. Oxamyl application consistently and significantly ($P = 0.014$) increased the number of tubers produced in the 40-60mm grade but did not affect the tuber numbers in either the <40mm or the total numbers of tubers produced. The no fertiliser treatment, with or without oxamyl, produced the lowest number of tubers in the ware grade (40-60mm) (Table 3.10).

ii) Tolerance ratio

There were no significant effects of oxamyl or fertiliser application type on the tolerance ratios (see Table 3.11 for explanation) of plants from plots either treated with oxamyl or not. Where all of the fertiliser was applied as broadcast granules to plots not treated with oxamyl, a lower tolerance ratio was achieved than where the fertiliser was split between broadcast granular and foliar NPK, but this was not significant (Table 3.11).

Table 3.9. The effects of fertiliser application type, foliar NPK and nematicide on the yield (t/ha, 158 DAP) of potatoes infected by *Globodera pallida*.

fertiliser method	<40 mm grade -O[a]	<40 mm grade +O	<40 mm grade method means	40-60 mm grade -O	40-60 mm grade +O	40-60 mm grade method means	total yield -O	total yield +O	total yield method means
NF[b]	13.3	10.7	12.0	11.6	19.4	15.5	24.9	30.2	27.5
BF	11.1	10.8	10.9	21.4	23.4	22.4	32.7	34.3	33.5
BF+F	11.4	11.4	11.4	22.0	23.8	22.9	33.8	35.8	34.8
LF	10.4	10.3	10.3	23.5	23.7	23.6	34.6	34.3	34.5
LF+F	11.0	10.6	10.8	22.7	26.0	24.3	34.2	37.2	35.7
oxamyl means	11.4	10.8		20.2	23.3		32.0	34.3	

	SED	Significance (P =)	d.f.	CV %
$\leq$ 40mm grade.				
oxamyl means	0.48	n.s.	16	
method means	1.12	n.s.	16	
oxamyl*method	1.36	n.s.	28	15.4
oxamyl*method# [c]	1.08			
40-60mm grade				
oxamyl means	1.47	n.s. (0.056)	16	
method means	3.60	n.s.	16	
oxamyl*method	4.28	n.s.	28	23.9
oxamyl*method#	3.28			
total yield				
oxamyl means	1.29	n.s.	16	
method means	3.70	n.s.	16	
oxamyl*method	4.23	n.s.	25	13.8
oxamyl*method#	2.89			

[a] - O = without oxamyl, + O = with oxamyl.

[b] see Table 3.1.

[c] (# when comparing within the same fertiliser method)

Table 3.10. The effects of fertiliser application type, foliar NPK and nematicide on the number of tubers produced (158 DAP) by potatoes infected by *Globodera pallida.*

fertiliser method	<40 mm grade			40-60 mm grade			total number		
	-O[a]	+O	method means	-O	+O	method means	-O	+O	method means
NF[b]	382	287	335	132	185	159	515	472	494
BF	317	300	309	200	231	216	518	531	524
BF+F	287	307	297	200	227	214	487	534	511
LF	279	277	278	221	224	223	500	501	500
LF+F	283	268	276	203	236	220	487	504	495
oxamyl means	310	288		192	221		501	508	

<u>< 40mm grade.</u>	SED	Significance (P =)	d.f.	CV %
oxamyl means	17.5	n.s.	16	
method means	33.5	n.s.	16	
oxamyl*method	43.4	n.s.	32	20.7
oxamyl*method# [c]	39.0			
<u>40-60mm grade</u>				
oxamyl means	10.5	0.014	16	
method means	26.6	n.s.	16	
oxamyl*method	31.4	n.s.	32	18.0
oxamyl*method#	23.5			
<u>total number</u>				
oxamyl means	17.1	n.s.	16	
method means	36.6	n.s.	16	
oxamyl*method	45.5	n.s.	32	12.0
oxamyl*method#	38.3			

[a] - O = without oxamyl, + O = with oxamyl.

[b] see Table 3.1.

[c] (# when comparing within the same fertiliser method)

Table 3.11. The effects of fertiliser application type, foliar NPK and nematicide on the yield (t/ha, 158 DAP) and tolerance of potatoes infected by *Globodera pallida*.

fertiliser method	total yield (t/ha) without oxamyl	total yield (t/ha) with oxamyl	tolerance ratio without oxamyl	tolerance ratio with oxamyl	tolerance ratio method means
NF [a]	24.9	30.2	0.73	0.88	0.80
BF	32.7	34.3	0.95	1.00	0.98
BF+F	33.8	35.8	0.99	1.05	1.02
LF	34.6	34.3	1.01	1.00	1.01
LF+F	34.2	37.2	1.00	1.08	1.04
oxamyl means			0.94	1.00	

tolerance ratio	SED	Significance (P =)	d.f.	CV %
oxamyl means	0.038	n.s.	16	
method means	0.108	n.s.	16	
oxamyl*method	0.123	n.s.	25	13.8
oxamyl*method# [b]	0.084			

[a] see Table 3.1.

[b] (# when comparing within the same fertiliser method)

Tolerance ratios were derived as a ratio of a treatment yield to the mean yield of both broadcast and liquid fertiliser treatments which had received oxamyl but no foliar N, P or K applications (potentially giving the normal yield of a potato crop in the absence of PCN).

3.4 Results of experiment two

The effects of individual and combined applications of foliar NPK on the growth and yield of potatoes infected by the potato cyst nematode, *Globodera pallida.*

3.4.1 PCN populations

The PCN population in the experimental area was identified by isoelectric focusing as *G. pallida* with no indication of presence of *G. rostochiensis.*

i) Initial population density

The initial PCN population densities (Pi, eggs/g soil) did not differ significantly between the experimental treatments (Table 3.12), so no individual treatment was under significantly higher or lower PCN pressure than any other. The mean PCN population was 13 eggs/g soil. The CV of 53.4%, however, suggests that there was substantial variation across the experimental area.

ii) Final population density

The final PCN population densities (Pf, eggs/g soil) were not significantly affected by any of the foliar applications. The mean Pf of all plots which had received oxamyl, 195 eggs/g soil, was not significantly less than the Pf of plots which had not been treated with oxamyl, 208 eggs/g soil, demonstrating no overall reduction of PCN population development from oxamyl application (Table 3.12).

iii) Pf/Pi ratios

The ratio of PCN multiplication, Pf/Pi, required $\log_e$ transformation of the values to achieve the normal distribution of data necessary for analysis of variance. The $\log_e$ Pf/Pi values were not significantly affected by foliar nutrient or oxamyl applications (Table 3.13).

Table 3.12. The initial (Pi) and final (Pf) population densities of PCN in an investigation of the effects of individual and combined applications of foliar fertiliser on the growth and yield of potatoes infected by *Globodera pallida.*

foliar nutrient	Pi (eggs/g soil) without oxamyl	Pi (eggs/g soil) with oxamyl	Pi (eggs/g soil) foliar means	Pf (eggs/g soil) without oxamyl	Pf (eggs/g soil) with oxamyl	Pf (eggs/g soil) foliar means
Std + FW [a]	12	14	13	187	172	180
Std + Fol N	8	13	10	227	186	206
Std + Fol P	17	13	15	199	218	208
Std + Fol K	11	14	12	263	158	210
Std + Fol NP	12	12	12	198	156	177
Std + Fol NK	13	15	14	204	239	221
Std + Fol KP	13	11	12	192	252	222
Std + Fol NPK	15	14	14	190	176	183
oxamyl means	12	13		208	195	

<u>Pi</u>	SED	significance (P =)	d.f.	CV %
oxamyl means	1.5	n.s.	32	
foliar means	2.3	n.s.	28	
oxamyl*foliar	3.8	n.s.	58	53.4
oxamyl*foliar# [b]	4.3			
<u>Pf</u>				
oxamyl means	15.0	n.s.	32	
foliar means	26.2	n.s.	28	
oxamyl*foliar	39.8	n.s.	60	33.3
oxamyl*foliar#	42.3			

[a] see Table 3.2.

[b] (# when comparing within the same fertiliser method)

3.4.2 Potato root invasion by PCN

The numbers of PCN juveniles, all stages, counted in the stained potato roots at 80 DAP were not significantly affected by the foliar nutrient applications that had been made by this time. There was little evidence that oxamyl had reduced PCN invasion with means of 240 and 284 juveniles/g root respectively in plants from plots treated or untreated with oxamyl (Table 3.13). An almost normal distribution was shown with the root invasion values negating the need for transformation, however, a $\log_e$ transformation did lower the CV to 17.2 % but did not affect the significance (values are therefore not given).

3.4.3 Plant growth

i) Emergence

There were no significant differences in the rate of plant emergence. Oxamyl application showed weak ($P = 0.056$) evidence of an increase in the overall rate of plant emergence but, as no foliar nutrient applications had been made at this time, the variation in the rate of emergence in plots destined for individual foliar nutrient treatments suggests that the oxamyl effect was inconsistent (Table 3.14).

ii) Plant fresh-weight

Plant fresh-weights, taken at 80 DAP and after two applications of foliar nutrients, showed that oxamyl application had significantly increased the whole-plant ($P = 0.01$) and above- ground biomass ($P < 0.001$) but that there were no significant effects on the fresh-weight of roots or tubers. No significant effects arose from application of the foliar nutrients. However, the application of foliar K plus P produced the largest effects on the whole-plant, above-ground and root weights in plots not treated with oxamyl, with values approaching or exceeding those obtained in the standard treatment receiving oxamyl (Tables 3.15a and 3.15b).

Table 3.14. The effects of individual and combined applications of foliar fertilisers on the percentage emergence at 40 DAP, of potatoes infected by *Globodera pallida.*

Foliar nutrient	without oxamyl	with oxamyl	foliar means
Std + FW [a]	26.4	29.6	28.0
Std + Fol N	29.4	27.8	28.6
Std + Fol P	29.2	29.6	29.4
Std + Fol K	28.6	27.4	27.4
Std + Fol NP	24.6	28.6	28.6
Std + Fol NK	26.4	30.0	30.0
Std + Fol KP	30.0	27.6	27.6
Std + Fol NPK	27.8	30.8	30.8
oxamyl means	27.8	28.92	

	SED	significance (P =)	d.f.	CV %
oxamyl means	0.57	n.s. (0.056)	32	
foliar means	1.21	n.s.	28	
oxamyl*foliar	1.66	n.s.	60	9.0
oxamyl*foliar#	1.61			

(# when comparing within the same fertiliser method)

[a] see Table 3.2.

iii) Percentage ground cover

a) 66 DAP

Applying oxamyl significantly ($P = 0.009$) increased percentage ground cover at 10 days after the first application of foliar nutrients, whilst overall foliar treatment means also showed significant ($P = 0.027$) ground cover reductions where foliar N plus K and foliar K plus P had been applied. In plots not treated with oxamyl the application of foliar P and foliar NPK gave percentage ground cover which compared favourably to the Std + FW treatment with oxamyl (Table 3.16).

Table 3.15a The effects of individual and combined applications of foliar fertilisers on plant fresh-weights at 80 DAP, of potatoes infected by *Globodera pallida.*

foliar nutrient	whole plant wt (g) without oxamyl	whole plant wt (g) with oxamyl	whole plant wt (g) foliar means	above ground wt (g) without oxamyl	above ground wt (g) with oxamyl	above ground wt (g) foliar means
Std + FW [a]	900	1080	990	548	756	652
Std + Fol N	996	1026	1011	643	688	665
Std + Fol P	839	931	885	502	622	562
Std + Fol K	944	861	903	591	543	567
Std + Fol NP	843	1091	967	505	726	615
Std + Fol NK	889	1014	952	558	674	616
Std + Fol KP	1022	1145	1084	667	768	717
Std + Fol NPK	819	998	909	521	673	597
oxamyl means	907	1018		567	681	

whole plant	SED	significance (P =)	d.f.	CV %
oxamyl means	40.6	0.010	32	
foliar means	72.5	n.s.	28	
oxamyl*foliar	108.8	n.s.	60	18.9
oxamyl*foliar# [b]	114.9			
above ground				
oxamyl means	29.4	<0.001	32	
foliar means	60.2	n.s.	28	
oxamyl*foliar	84.2	n.s.	60	21.1
oxamyl*foliar#	83.2			

[a] see Table 3.2.

[b] (# when comparing within the same fertiliser method)

Table 3.15b The effects of individual and combined applications of foliar fertilisers on plant fresh-weight at 80 DAP, of potatoes infected by *Globodera pallida*.

	root wt (g)			tuber wt (g)		
foliar nutrient	without oxamyl	with oxamyl	foliar means	without oxamyl	with oxamyl	foliar means
Std + FW [a]	10.2	11.7	11.0	307	274	290
Std + Fol N	12.5	11.3	11.9	304	288	296
Std + Fol P	10.4	10.7	10.5	288	252	270
Std + Fol K	12.6	12.1	12.4	297	271	284
Std + Fol NP	10.3	12.9	11.6	293	308	301
Std + Fol NK	11.4	11.0	11.2	283	292	287
Std + Fol KP	13.2	13.8	13.5	300	320	310
Std + Fol NPK	12.7	12.3	12.5	249	267	258
oxamyl means	11.7	12.0		290	284	

<u>root wt</u>	SED	significance (P =)	d.f.	CV %
oxamyl means	0.64	n.s.	32	
foliar means	1.34	n.s.	28	
oxamyl*foliar	1.85	n.s.	60	24.3
oxamyl*foliar# [b]	1.82			
<u>tuber wt</u>				
oxamyl means	15.3	n.s.	32	
foliar means	23.0	n.s.	28	
oxamyl*foliar	38.3	n.s.	58	23.9
oxamyl*foliar#	43.3			

[a] see Table 3.2.

[b] (# when comparing within the same fertiliser method)

Table 3.16. The effects of individual and combined applications of foliar fertilisers on the percentage ground cover at 66 and 108 DAP, of potatoes infected by *Globodera pallida*.

foliar nutrient	66 DAP without oxamyl	66 DAP with oxamyl	66 DAP foliar means	108 DAP (arcsine transformed) without oxamyl	108 DAP (arcsine transformed) with oxamyl	108 DAP (arcsine transformed) foliar means
Std + FW [a]	56.2	59.2	57.7	79.2	88.8	84.1
Std + Fol N	55.4	61.0	58.2	77.8	83.3	80.5
Std + Fol P	59.6	57.2	58.4	74.1	85.2	79.6
Std + Fol K	56.8	63.4	60.1	79.0	80.2	79.6
Std + Fol NP	57.0	54.2	55.6	77.6	85.8	81.7
Std + Fol NK	49.6	57.6	53.6	81.8	83.1	82.5
Std + Fol KP	55.0	61.4	58.2	76.8	86.1	81.4
Std + Fol NPK	60.0	62.0	61.0	80.2	86.4	83.3
oxamyl means	56.2	59.5		78.3	84.8	

	SED	significance (P =)	d.f.	CV %
<u>66 DAP</u>				
oxamyl means	1.19	0.009	28	
foliar means	2.01	0.027	28	
oxamyl*foliar	3.12	n.s.	55	9.2
oxamyl*foliar# [b]	3.37			
<u>108 DAP</u>				
oxamyl means	1.16	<0.001	28	
foliar means	2.07	n.s.	28	
oxamyl*foliar	3.11	n.s.	55	6.4
oxamyl*foliar#	3.28			

[a] see Table 3.2.

[b] (# when comparing within the same fertiliser method)

b) 108 DAP

Percentage ground cover at 108 DAP was estimated six days after the fourth application of foliar nutrients. Oxamyl treated plots had significantly ($P<0.001$) and consistently higher percentage ground cover from all foliar nutrient treatments compared with plots not treated with oxamyl. There were no significant effects from foliar nutrient application and, except for foliar N plus K and foliar NPK, it appears that foliar nutrients depressed ground cover in plots not treated with oxamyl below that achieved by the standard treatment with no foliar nutrient applications (Table 3.16).

iv) Leaf area index

a) 110 DAP

Leaf area index was estimated at 110 DAP, the day of the last application of foliar nutrients. Oxamyl application significantly ($P = 0.010$) improved leaf area index overall. In plots which had not been treated with oxamyl the application of foliar N gave a leaf area index which was a) much greater (4.80) than that achieved by all other foliar nutrient applications (mean = 3.92), and b) greater than the leaf area index achieved by the Std + FW treatment which had been treated with oxamyl (4.64). These differences were, however, not significant (Table 3.17).

b) 131 DAP

The leaf area index was estimated at this time in order to determine the effects of the foliar nutrient treatments on canopy development in relation to the Std + FW treatment plus oxamyl. Where oxamyl had been applied an overall significant ($P = 0.029$) benefit to leaf area index was achieved, but the benefit was not consistent over individual foliar nutrient treatments. The mean values of foliar nutrient treatments showed that there was significant ($P = 0.005$) benefits to leaf area index from the application of foliar N. In fact, in plots not treated with oxamyl, only plants receiving the foliar N treatment retained a leaf area index similar to that found with the Std + FW treatment which had been treated with oxamyl, but the difference from other treatments was not significant (Table 3.17).

Table 3.17. The effects of individual and combined applications of foliar fertilisers on the leaf area index (LAI) at 110 and 131 DAP, of potatoes infected by *Globodera pallida*.

	110 DAP			131 DAP		
foliar nutrient	without oxamyl	with oxamyl	foliar means	without oxamyl	with oxamyl	foliar means
Std + FW [a]	3.77	4.64	4.21	2.01	2.96	2.49
Std + Fol N	4.80	4.73	4.76	2.77	3.08	2.93
Std + Fol P	3.51	4.06	3.79	1.86	1.69	1.77
Std + Fol K	3.76	3.54	3.65	2.19	2.19	2.19
Std + Fol NP	3.60	4.38	3.99	1.84	2.18	2.01
Std + Fol NK	4.13	4.46	4.29	1.92	2.30	2.11
Std + Fol KP	3.81	4.38	4.09	2.20	2.62	2.41
Std + Fol NPK	3.95	4.29	4.12	2.39	2.53	2.46
oxamyl means	3.92	4.31		2.15	2.44	

<u>110 DAP</u>	SED	significance (P =)	d.f.	CV %
oxamyl means	0.14	0.010	28	
foliar means	0.31	n.s. (0.054)	28	
oxamyl*foliar	0.43	n.s.	55	15.6
oxamyl*foliar# [b]	0.41			
<u>131 DAP</u>				
oxamyl means	0.123	0.029	28	
foliar means	0.253	0.005	27	
oxamyl*foliar	0.360	n.s.	55	24.9
oxamyl*foliar#	0.362			

[a] see Table 3.2.

[b] (# when comparing within the same fertiliser method)

3.4.4 Plant nutrient status

i) Nitrogen

The percentage N found in the whole plant dry matter, measured at nine days after the second application of foliar nutrients, showed significant (P = 0.006) benefits from oxamyl application.

The mean values of foliar nutrient treatments showed significant (P = 0.048) reductions in N concentration where foliar K, NP and NK were applied compared with the Std + FW treatment. In plots not treated with oxamyl, only the applications of foliar N and foliar KP gave N concentrations greater than in the Std + FW plots not treated with oxamyl. These were not significant improvements, however, and the concentrations were below those measured in the Std + FW treatment treated with oxamyl (Table 3.18).

ii) Phosphorus

The percentage P found in whole plant dry matter was consistently and significantly (P<0.001) increased where oxamyl had been applied to plots. The mean values of foliar treatments showed significantly (P = 0.037) higher P concentrations in the Std + FW and Std + foliar KP treatments than in all other treatments. In plots not treated with oxamyl, only applications of foliar KP resulted in P concentrations which were similar to the P concentration measured in the Std + FW treatment receiving oxamyl. Surprisingly, the application of foliar P to plants in plots not treated with oxamyl resulted in a much reduced concentration of P in the plant dry matter, but this reduction was not significant.

iii) Potassium

There were no significant differences in the percentage K found in plant dry matter arising from foliar nutrient application. Oxamyl application, however, showed slightly but not significantly (P = 0.058) higher K concentrations. In plots not treated with oxamyl, only the application of foliar KP resulted in a K concentrations above that seen with the Std + FW treated plots which had also been treated with oxamyl.

Table 3.18. The effects of individual and combined applications of foliar fertilisers on the nutrient status of whole potato plants infected by *Globodera pallida*, measured 82 DAP (nine days after the second foliar application).

foliar nutrient	% N in d.m.			% P in d.m.			% K in d.m.		
	- O [a]	+ O	mean	- O	+ O	mean	- O	+ O	mean
Std + FW [a]	3.31	3.44	3.37	0.269	0.296	0.282	5.21	5.23	5.22
Std + Fol N	3.37	3.30	3.33	0.264	0.278	0.271	5.10	5.12	5.11
Std + Fol P	3.18	3.36	3.27	0.235	0.276	0.255	4.79	4.94	4.86
Std + Fol K	3.21	3.17	3.19	0.249	0.250	0.249	4.99	4.94	4.97
Std + Fol NP	3.09	3.32	3.21	0.249	0.259	0.254	4.80	5.21	5.01
Std + Fol NK	3.09	3.30	3.19	0.234	0.274	0.254	4.84	5.40	5.12
Std + Fol KP	3.33	3.38	3.35	0.290	0.296	0.293	5.43	5.45	5.44
Std + Fol NPK	3.23	3.43	3.33	0.254	0.286	0.270	4.87	5.15	5.01
oxamyl means	3.22	3.34		0.255	0.277		5.00	5.18	

	SED	significance (P =)	d.f.	CV %
<u>% N in d.m.</u>				
oxamyl means	0.038	0.006	32	
foliar means	0.069	0.048	28	
oxamyl*foliar	0.103	n.s.	60	5.2
oxamyl*foliar# [c]	0.108			
<u>% P in d.m.</u>				
oxamyl means	0.0054	<0.001	32	
foliar means	0.0138	0.037	28	
oxamyl*foliar	0.0175	n.s.	55	9.0
oxamyl*foliar#	0.0151			
<u>% K in d.m.</u>				
oxamyl means	0.090	n.s.(0.058)	32	
foliar means	0.212	n.s.	28	
oxamyl*foliar	0.278	n.s.	57	7.9
oxamyl*foliar#	0.253			

[a] - O = without oxamyl, + O = with oxamyl.

[b] see Table 3.2.

[c] (# when comparing within the same fertiliser method)

3.4.5 Tuber yield

Applying oxamyl gave significant benefits in all three tuber size grades: in the <40mm grade oxamyl significantly ($P = 0.031$) reduced yield; in the 40-60 mm grade and total tuber yield oxamyl significantly ($P = 0.002$ and $P = 0.007$, respectively) increased yield (Table 3.19). The mean of foliar treatments showed significant ($P = 0.032$) total yield benefits from the application of foliar N and foliar NK and weak evidence ($P = 0.059$) of yield benefits in the 40-60mm grade. These same two treatments, foliar N and foliar NK, gave yields in plots not treated with oxamyl similar to or greater than the Std + FW treatment plus oxamyl, though the differences from other treatments were not significant.

i) Tuber number

The total numbers of tubers produced were not affected by oxamyl application, but oxamyl application significantly ($P = 0.006$) reduced the numbers of tubers in the <40mm grade and significantly ($P<0.001$) increased the number of tubers in the 40-60mm grade. All plots not treated with oxamyl produced more tubers than oxamyl treated plots in the <40mm grade but only the foliar N application gave similar numbers of tubers in the 40-60mm grade to the Std + FW treatment which had been treated with oxamyl. Foliar nutrient applications did not significantly affect the total numbers of tubers produced but the greatest number was produced where foliar P had been applied to plots treated with oxamyl (Table 3.20).

Table 3.19. The effects of individual and combined applications of foliar fertilisers on the yield (t/ha, 150 DAP) of potatoes infected by *Globodera pallida*.

foliar nutrient	<40 mm grade -O[a]	<40 mm grade +O	<40 mm grade means	40-60 mm grade -O	40-60 mm grade +O	40-60 mm grade means	total yield -O	total yield +O	total yield means
Std + FW[a]	12.5	11.8	12.1	25.5	30.5	28.0	38.4	42.8	40.6
Std + Fol N	12.2	12.2	12.2	30.7	31.6	31.1	43.9	44.7	44.3
Std + Fol P	12.4	13.5	13.0	23.1	27.5	25.3	36.4	41.3	38.9
Std + Fol K	12.7	11.9	12.3	25.0	23.9	24.5	38.1	36.1	37.1
Std + Fol NP	13.4	10.8	12.1	25.2	27.8	26.5	38.7	39.1	38.9
Std + Fol NK	14.4	12.1	13.2	28.9	29.4	29.2	43.8	42.7	43.3
Std + Fol KP	13.9	12.6	13.3	22.9	28.7	25.8	37.0	41.4	39.2
Std + Fol NPK	13.6	12.0	12.8	25.9	31.6	28.7	36.5	44.4	40.3
oxamyl means	13.1	12.1		25.9	28.9		39.1	41.5	

<u>< 40mm grade.</u>	SED	Significance (P =)	d.f.	CV %
oxamyl means	0.44	0.031	26	
foliar means	0.92	n.s.	28	
oxamyl*foliar	1.28	n.s.	54	15.7
oxamyl*foliar# [c]	1.25			
<u>40-60mm grade</u>				
oxamyl means	0.89	0.002	26	
foliar means	2.12	n.s.(0.059)	28	
oxamyl*foliar	2.77	n.s.	53	23.9
oxamyl*foliar#	2.52			
<u>total yield</u>				
oxamyl means	0.82	0.007	32	
foliar means	2.09	0.032	28	
oxamyl*foliar	2.65	n.s.	52	9.1
oxamyl*foliar#	2.32			

[a] - O = without oxamyl, + O = with oxamyl.

[b] see Table 3.2.

[c] (# when comparing within the same fertiliser method)

Table 3.20. The effects of individual and combined applications of foliar fertilisers on the numbers of tubers produced at harvest (150 DAP) by potatoes infected by *Globodera pallida*.

foliar nutrient	<40 mm grade			40-60 mm grade			total number		
	-O[a]	+O	means	-O	+O	means	-O	+O	means
Std + FW [a]	397	363	380	245	292	268	642	655	648
Std + Fol N	402	373	388	296	295	295	698	668	683
Std + Fol P	398	440	419	192	268	230	590	708	649
Std + Fol K	431	375	403	245	222	234	675	597	636
Std + Fol NP	403	329	366	215	263	239	618	592	605
Std + Fol NK	450	381	415	215	299	257	665	679	672
Std + Fol KP	441	413	427	250	288	269	691	701	696
Std + Fol NPK	428	365	397	256	300	278	684	665	675
oxamyl means	419	380		239	278		658	658	

	SED	Significance (P =)	d.f.	CV %
<u>≤ 40mm grade.</u>				
oxamyl means	13.1	0.006	32	
foliar means	30.9	n.s.	28	
oxamyl*foliar	40.5	n.s.	57	12.2
oxamyl*foliar# [c]	37.0			
<u>40-60mm grade</u>				
oxamyl means	10.7	<0.001	32	
foliar means	21.6	n.s.(0.054)	28	
oxamyl*foliar	30.4	n.s.	60	18.5
oxamyl*foliar#	30.2			
<u>total number</u>				
oxamyl means	15.9	n.s.	32	
foliar means	35.2	n.s.	28	
oxamyl*foliar	47.4	n.s.	60	10.8
oxamyl*foliar#	45.0			

[a] - O = without oxamyl, + O = with oxamyl.
[b] see Table 3.2.
[c] (# when comparing within the same fertiliser method)

Table 3.21. The effects of individual and combined applications of foliar fertilisers on the yield (t/ha, 150 DAP) and tolerance of potatoes infected by *Globodera pallida*.

foliar nutrient	total yield (t/ha) without oxamyl	total yield (t/ha) with oxamyl	tolerance ratio without oxamyl	tolerance ratio with oxamyl	tolerance ratio foliar means
Std + FW [a]	38.4	42.8	0.90	1.00	0.95
Std + Fol N	43.9	44.7	1.02	1.04	1.03
Std + Fol P	36.4	41.3	0.85	0.97	0.91
Std + Fol K	38.1	36.1	0.89	0.84	0.87
Std + Fol NP	38.7	39.1	0.91	0.91	0.91
Std + Fol NK	43.8	42.7	1.02	1.00	1.01
Std + Fol KP	37.0	41.4	0.86	0.97	0.92
Std + Fol NPK	36.5	44.1	0.85	1.03	0.94
oxamyl means	39.1	41.5	0.91	0.97	

tolerance ratio	SED	Significance (P =)	d.f.	CV %
oxamyl means	0.019	0.007	26	
foliar means	0.049	0.032	28	
oxamyl*foliar	0.062	n.s.	52	9.1
oxamyl*foliar# [b]	0.054			

[a] see Table 3.2.

[b] (# when comparing within the same fertiliser method)

ii) Tolerance ratio

The tolerance ratio was calculated by expressing the individual treatment mean yield as a percentage of the yield of the Std + FW treatment which had been treated with oxamyl. In plots not treated with oxamyl the Std + FW treatment gave a ratio of 0.90, which in effect is the tolerance level of this cultivar in this specific environment. The foliar nutrient applications which improved on this tolerance level (0.90) in plots not treated with oxamyl were foliar N and foliar NK, which attained equivalent ratios of 1.02 (Table 3.21). Where the means for plots with or without oxamyl were calculated a significant ($P = 0.007$) tolerance benefit was seen from oxamyl application.

3.5 General observations and environmental monitoring

Low air temperatures after the crop was planted, which reached a minimum of 2 °C (Figure 3.1) at 19 DAP, prevented soil temperatures from rising above 7.5 °C by this date and, accompanied by the use of unchitted seed, caused a long delay before plant emergence (28% at 40 DAP). Soil temperatures over the season were a minimum of 7.5 °C, a maximum of 23.7 °C and averaged 15.2 °C. Irrigation was aimed at maintenance of soil moisture deficits of 25mm and this was achieved throughout the majority of the growing period-until 110 DAP, when the crop surrounding the experimental site was harvested and the centre pivot irrigation system, not suited to irrigation of small areas, could no longer be used (Figure 3.2). During the growing period a weed control problem (*Galium aparine*) was encountered, requiring hand removal of the weeds which resulted in damage to plants within a few plots. These plots were not used for data acquisition from that point onwards.

One of the potential problems of applying foliar fertilisers is the leaf damage (scorch) which can result from their application. The leaf surfaces were monitored for such damage one, two and seven days after the nutrient applications. There were no visible signs that any of the nutrient applications had caused damage to the leaf surfaces.

Tuber quality at harvest was poor with severe growth cracking. An effect noted as early as tuber initiation. Inspection of 20 test points across the experimental area and the surrounding crop revealed that this problem had occurred in all of the crop.

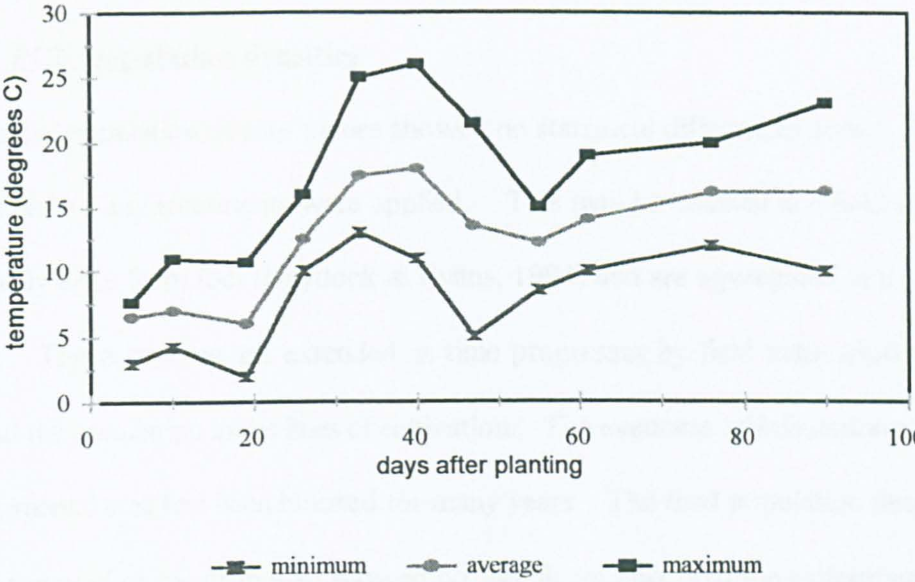

Figure 3.1. Air temperature at one metre above ground level at the field experiment site, Newport, Shropshire, 1996.

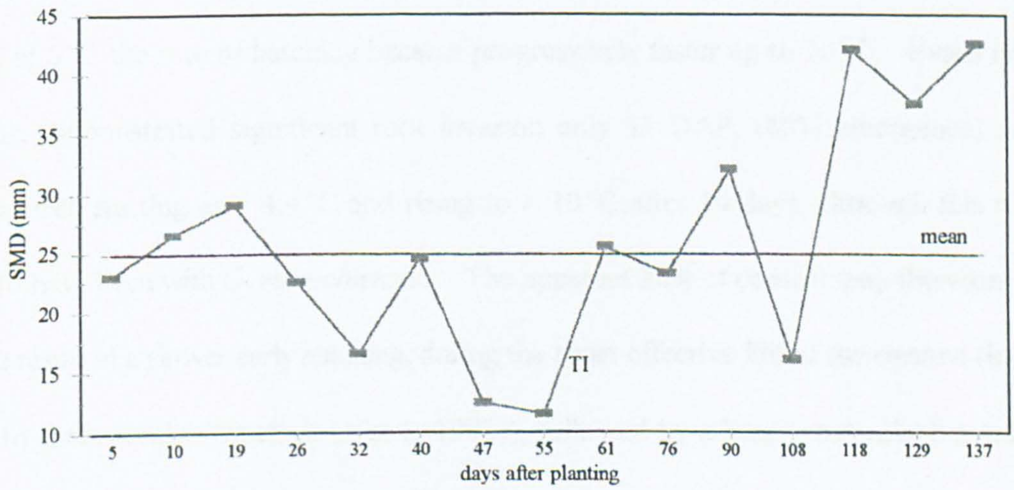

Figure 3.2. Mean soil moisture deficits, derived using an Institute of Hydrology neutron probe, for the 1996 experimental site at Newport, Shropshire. TI indicates the onset of tuber initiation.

3.6 Discussion of 1996 results

3.6.1 PCN population densities

The initial population density studies showed no statistical differences across the experimental areas before any treatments were applied. This may be unusual in a field situation as PCN normally arise from foci (Haydock & Evans, 1994) and are aggregated in patches across the field. These patches are extended as time progresses by field cultivation practices which spread the population in the lines of cultivation. The evenness of infestation suggests that the experimental area had been infested for many years. The final population densities measured after removal of the crop also showed no significant effects of the experimental treatments. This is unusual where comparisons were made between the none and full rate nematicide treatments as Whitehead *et al.* (1984) suggests that oxamyl application can minimise population increase. The low early season soil temperatures (minimum 7.5°C) may have been influential in slowing PCN hatch as Franco (1979) demonstrated that although *G. pallida* hatched at 5°C the rate of hatching became progressively faster up to 20°C. Evans (1969) however, demonstrated significant root invasion only 33 DAP, (60% emergence) at soil temperatures starting at > 4.4°C and rising to > 10°C after 14 days, although this is now known to have been with *G. rostochiensis*. The apparent lack of control may therefore have been the result of a slower early hatching, during the short effective life of the oxamyl (half life of one to three weeks (Smelt & Leistra, 1992)), followed by a later substantial hatch into a relatively oxamyl free environment (Whitehead, 1992). There are several other possible explanations for the poor control, which include inefficient oxamyl incorporation or a dilution of the oxamyl through incorporation to 35 cm depth with a rotary bed-tiller, as shown by Woods & Haydock (1995) and Woods (1997).

The population studies did give some interesting observations. In the experiment studying the effects of individual or combined applications of foliar NPK, the Pf/Pi ratios showed considerable multiplication where foliar N and foliar K had been applied to plots not treated with oxamyl, although there were no significant differences. The application of foliar P and foliar KP also showed high multiplication rates but this was in plots treated with oxamyl. A similar increase in multiplication has been shown by Raispere (1990), who found that high rates of N (6 times normal) inhibited PCN development whereas at lower rates of N and P there was an increase in the development and size of the females. Where the foliar application contained the three nutrients N, P and K, the Pf/Pi ratio in the non nematicide treatments was found to be much lower than that calculated for plots treated with oxamyl, whereas in the method of fertiliser application experiment the Pf/Pi's were similar in both oxamyl treated and untreated plots. As the method of fertiliser application experiment used nutrient levels in line with ADAS (1994) recommendations and the individual or combinations of foliar NPK experiment used 25% more nutrients, the higher total NPK supply on nematicide treated plots could have benefited multiplication by interactions between the nutrient status of the plant and the nematode.

3.6.2 Plant emergence

The rate of plant emergence, measured at 40 DAP, was consistently improved by oxamyl application in the fertiliser application method experiment. This would suggest that, as the root invasion was also significantly reduced, the nematode infection of the plant had restricted the early plant development as shown by Van der Wal (1978). Fertiliser application methods did not affect the rate of plant emergence in plots not treated with oxamyl, suggesting that neither broadcast granular nor liquid placement of fertilisers had any advantage over the others. In the experiment investigating the effect of individual or combined applications of foliar NPK, oxamyl did not increase the rate of plant emergence and, as no foliar nutrients had been applied by 40 DAP, the variation in the rates of plant emergence could not be attributed to these treatments. The CV of 9.0 % would also suggest that there was only a small amount of variation within the experiment. It can only be concluded that the oxamyl effect was poor in this experiment, a conclusion supported by the root invasion data.

3.6.3 Root invasion

Although the PCN population development was not reduced by oxamyl application in either of the experiments there was evidence to suggest that root invasion had been affected in one experiment. There were significantly ($P = 0.003$) fewer PCN juveniles in plant roots from oxamyl treated plots in the method of fertiliser application experiment but this was not seen in the foliar NPK experiment. The timing of the sample removal from the experiment may be very important in these results. The mean number of juveniles per g root (524) found in the method of application experiment contained all stages of juvenile development, whereas most of the 262 per g root found in the foliar NPK experiment were of 3rd, 4th and 5th stage nematodes. It would be reasonable to suggest, therefore, that as the samples from the foliar NPK experiment were taken 11 days later than in the application method experiment, many of the 5th stage males had migrated out of the roots into the surrounding soil.

3.6.4 Plant fresh-weight

In the fertiliser application method experiment, the total, above-ground plant biomass and tuber weight, at 69 DAP, was significantly ($P < 0.05$) higher in plants from oxamyl treated plots, which is a typical response (Trudgill *et al.*, 1975a, 1975b), when plants come from plots treated with oxamyl. The responses of the root weights to the different methods of fertiliser application, although showing no significant differences, were interesting. When all of the fertiliser was applied to the seedbed, as either broadcast granular or liquid placed, root weights were less where no oxamyl had been applied. This would be expected, as Evans, Trudgill & Brown (1977) amongst other, have demonstrated inhibition of root growth where plants are infected by PCN. However, when part of the fertiliser was applied by the foliar route an increase in root growth occurred, and this was marked where the foliar applications were in conjunction with broadcast granular applications. This was also the case with total and above-ground plant biomass, where the response was more pronounced when the foliar fertilisers were applied in conjunction with broadcast granular applications. Roy & Seth (1970) found a similar response, in plants not infected by PCN, where an improved top growth was accompanied by an increase in root weight. They suggested that the increased root size led to increased ability to take up nutrients from the soil, thus promoting further top growth. In this experiment, it is suggested that reducing the quantity of broadcast granular fertiliser in the seedbed, and providing nutrients to plant foliage, meant that the plants were of a suitable nutrient status for enhancement of root growth in search of soil nutrients, which were less prolific due to the reduced granular application.

In the foliar NPK experiment the application of foliar N, foliar K, and foliar KP led to increased (but not significantly) whole-plant, above-ground and root fresh-weights, in plots not treated with oxamyl. This may mean that these nutrients were limiting in the PCN infected plants but, as the number of PCN juveniles found in the roots were similar in both oxamyl treated and untreated plots, this is unlikely.

3.6.5 Percentage ground cover

The first ground cover assessments in both experiments, at 61 and 66 DAP, demonstrated a significant benefit from the application of oxamyl. This should have improved eventual crop yields as early crop canopy development intercepts more of the May to July incident radiation in the UK, which Allen and Scott (1992) suggest is more beneficial to yield than increased canopy size in the latter part of the season. The experiment with applications of foliar NPK also gave significant differences in percentage ground cover between the main treatments. This, unfortunately, gives little information of value as these differences are based on the mean of non and full rate nematicide treatments and, in some cases, the lack of ground cover in one part of the mean is overshadowed by high values in the other part of the mean, e.g. treatment four-foliar K applications. As no significant interactions were found it is unwise to speculate too much on any of the observations but it is perhaps worthy of note that foliar P and foliar N+P gave the highest percentage ground cover in the plots not treated with oxamyl. At this stage of growth (61 - 66 DAP) the requirement for P is high in potato crops, emphasised by Watson and Wilson (1956), who suggested that applications of P benefited early leaf area. This may indicate that P is limiting during early growth of PCN infected plants.

The second assessments of ground cover between 102 and 108 DAP were difficult to analyse due to many observations of 100% values. Gomez and Gomez (1984) suggest three rules to apply when analysing percentage data of which the second or third could be said to apply here : Rule 2, for percentage data that lie between 0 and 30 or 70 and 100, but not both, the square root transformation should be used; Rule 3, for percentage data that do not follow the ranges specified in rules one and two, the arcsine transformation should be used. For this reason the arcsine transformation was chosen as the most appropriate for the data in question. In the fertiliser application method experiment, applying part of the fertiliser by the foliar route in conjunction with liquid placed fertiliser produced the highest percentage ground cover for all plots not treated with oxamyl. This fertiliser application method produced ground cover equivalent to that found for broadcast granular fertiliser plots treated with oxamyl. There were no real ground cover improvements by any of the individual or combined applications of foliar NPK at this time.

3.6.6 Leaf area index

The leaf area index was only measured in the foliar NPK experiment. Leaf area index measurement at 110 DAP showed that the application of foliar P resulted in reduced leaf area, whereas applications of foliar N benefited leaf area, though not significantly. The leaf area at 131 DAP showed a significant benefit from nematicide and highly significant main treatment differences in favour of the foliar N application. There is strong evidence from Millard and Marshall (1986) regarding the benefits to leaf area duration from applications of N, which is also supported by Beukema and Van Der Zaag (1990) who emphasise the extension of haulm persistence when additional nitrogen is given. Applications of foliar P produced the lowest leaf areas at 131 DAP, which is again consistent with other findings, such as those of Watson and Wilson (1956), who suggest that the effect on the later stages of growth from applications of P is to cause an early senescence of the leaves and haulm. The applications of K, however, were of no benefit to the LAI on either assessment date and reduced the LAI in nematicide treated plots well below that seen in the control full rate nematicide treatment. This is in contrast to Watson and Wilson (1956), who suggest that applications of K can increase haulm persistence through the growing season. These observations do perhaps emphasise the plant's differing requirements for the three macro nutrients over the growing season and suggest that for foliar applications to be beneficial to the LAI, and thus the yield, a more tailored approach to the applications may be required.

3.6.7 Plant nutrient status

In the method of fertiliser application experiment, plants from plots not treated with oxamyl did not contain significantly lower concentrations of N, P or K, in contrast to the findings of several researchers (Trudgill *et al.*, 1975b; Fatemy & Evans, 1986a). The low soil infestation levels of PCN recorded in this experiment were shown not to have severely restricted root growth and would therefore not have significantly reduced the nutrient uptake capabilities of the plants. The most interesting, and relevant, observations from this experiment, however, are the differences in the plant concentrations of N, P and K arising from the fertiliser application methods themselves. Where all of the fertiliser was applied to the seedbed the liquid placement of the fertiliser resulted in much higher N and K concentrations, although the N and K concentrations were higher in plants from plots treated with oxamyl irrespective of fertiliser application method,. This would suggest that, although the liquid placement produced higher N and K concentrations within the plants, the differences of N and K concentration remained similar between the oxamyl treated and untreated, and that there was no actual alleviation of the nutrient deficit arising from PCN infection. Liquid fertiliser placement gave much higher P concentrations in the plants than found with broadcast granular applications but, unlike the response with N and K, the liquid placement resulted in similar P concentrations in plants from both oxamyl treated and untreated plots. It appears, therefore, that the liquid placement of the fertiliser not only increases the P concentration within the plant, as shown by Knittel (1988) and Lewis & Kettlewell (1992), but that this method can overcome the deficit of P arising from PCN infection of the plants. Substituting part of the liquid placed fertiliser by foliar applications to plants from plots not treated with oxamyl was also effective in giving N, P and K concentrations similar to those measured in plants from plots treated with oxamyl, suggesting that foliar application of these nutrients is effective at redressing the nutrient deficits from root uptake alone. With regard to these observations on nutrient uptake, it should be noted that, except in the case of the N concentration, there were no significant differences between treatments and therefore that no real conclusions can be reached from these results.

In the foliar NPK experiment, the comparisons of interest are all of foliar N, P and K applications to plants in plots not treated with oxamyl, as compared to standard fertiliser only applied to plants in oxamyl treated plots. In this experiment plants from plots not treated with oxamyl had lower concentrations of N and P than plants from plots treated with oxamyl, but there were no reductions of K concentration. When the nutrients were applied singly, only foliar N went some way to alleviate the deficit of the nutrient seen in plants from plots not treated with oxamyl. The applications of foliar P and foliar K resulted in concentrations not only lower than the standard fertiliser and oxamyl treatment but also lower than the concentrations in plants from the standard fertiliser not treated with oxamyl. It could be expected, as all three nutrients are effectively taken up by foliage (Gray, 1977), that the individual foliar applications of N, P and K would all result in increases of their respective nutrient concentrations above those found in plants where no foliar nutrients were applied. As only foliar N achieved this, whilst the foliar P and foliar K applications appeared to reduce the concentrations, it can only be assumed that the individual foliar P and foliar K applications were ineffective. In contrast to this, where foliar P and foliar K were applied together the resulting P and K concentrations in plants from plots not treated with oxamyl were increased to values similar to those found in the plants from the standard fertiliser plots treated with oxamyl. This association between the P and K is not widely discussed but Hart & Smith (1966) demonstrated that applications of soil-applied can K significantly increase the absorption of soil P by potatoes in some cases. The rectification of P and K deficits in PCN infected plants, by foliar fertilisers, may therefore require the application of both nutrients in order to be successful. The nutrient analysis of plant material in this experiment would suggest that N and P concentrations were reduced by PCN infection. The concentrations seen would not, however, be classed as deficient or limiting to crop growth.

3.6.8 Tuber yield

The yields from the fertiliser application method experiment showed no statistical differences in individual grades or in total yields. No benefits were seen from any fertiliser application, application type or the use of foliar NPK, which suggests that no fertiliser application method was more suited than any other for supplying nutrients to plants infected with PCN. Fertiliser applications would be expected to give some benefit to the yield by alleviating the expected nutrient deficiencies, as suggested by Trudgill *et al.* (1975a, 1975b). This lack of effect may have been due in part to the apparent lack of control seen from the oxamyl in the population studies but, as Trudgill *et al.* (1983) report, at low pre-planting PCN populations oxamyl has little effect on eventual yield. However, yield of 40-60mm grade tubers from the no fertiliser no oxamyl plots was very poor, so some benefit may have been gained from the use of the fertilisers. The tolerance ratios, expressed as a percentage of the mean yield achieved in the broadcast granular and liquid placed oxamyl treated plots, were all close to unity. No fertiliser application method could be said to have improved the tolerance of PCN infected potatoes.

In the foliar NPK experiment, the use of oxamyl significantly decreased the yield of <40mm grade tubers whilst significantly increasing the yield of 40-60mm grade and total yield, the increase in total yield coming from a higher proportion of 40-60mm ware grade tubers. The population study suggested no benefit of the oxamyl application on nematode reproduction oxamyl gave significant yield benefits. The applications of foliar N and foliar N+K both resulted in high total yields, when expressed as a mean of non and full rate oxamyl treatments, suggesting benefits from these two treatments. The lack of significance shown in the analysis of interactions suggests that the yields of plots receiving foliar nutrients did not vary with nematicide treatment. This may suggest some tolerance improvement as Evans and Franco (1979) and Evans (1982a) expressed tolerance on the basis of the ratio of yields of a cultivar in PCN infested and non-infested land. Where no significant difference occurred in yields of a main treatment between non and full rate nematicide treatments, therefore, the ratio would be close to unity and the tolerance level would be high. When tolerance ratios were calculated for total yields in this experiment, foliar N and foliar N+K both gave tolerance ratios in excess of unity thus suggesting tolerance improvements. When the yield increases from applications of foliar N are considered in conjunction with the LAI improvements, a relationship similar to previous research is seen. Trudgill (1987), working with *Globodera rostochiensis*, grafted a scion from the cultivar Cara, which shows vigorous top growth, onto Pentland Dell rootstocks and found a benefit to the yield from both an earlier attainment of 100% ground cover and extended haulm persistence. Haverkort *et al.* (1992) also indicate that cultivars which maintained ground cover well in the absence of nematodes (as is found with Cara) also do so in the presence of nematodes, which results in a greater interception of radiation and this, in turn, results in tolerance. The foliar N application could also be highlighting the deficiency of this nutrient in PCN infected plants as Haverkort *et al.* (1994) indicated that a lack of N was a major factor reducing yield. It was suggested that PCN invasion initially reduced root growth in the topsoil followed by the proliferation of roots in the same zone, but only after the N had been depleted during the early part of the growing season. The effects during the season were further aggravated by the reduced root density in the subsoil, caused by the PCN infestation, which would normally provide the plant with an adequate supply of N. In relation to the experiment carried out here with foliar N, therefore, the increased LAI could have been largely responsible for the tolerance improvements by alterations in the number and/or size of the canopy components and less reliance on the root system to supply nutrients. This would agree with current knowledge on the effect of increasing supplies of N which Marschner (1995) outlines as increasing the shoot/root ratios, leaf length, width and area. A further indication of the potential N deficiency in PCN infested plants comes from observations of effects that its deficiency has on inducing phytohormone changes. Kraus (1978) suggests that levels of abscisic acid (ABA) are increased where N is found to be deficient in potato plants. Therefore, the increased levels of ABA found in Pentland Dell infected by *Globodera rostochiensis* could be a result of N deficiency, rather than or in addition to the water stress proposed by Fatemy *et al.* (1985), with similar effects likely from infection by *G. pallida*. These areas warrant further investigation in relation to PCN infected plants.

There were also some interesting interactions in the experiment. Foliar K alone produced a higher yield in the non nematicide treatment than in the nematicide treatment but neither yield was particularly high. From the leaf area assessments it can be seen that the foliar K maintained a similar LAI to all other treatments at both assessment dates, except for the foliar N application which produced a greater LAI. Therefore, although foliar K maintained similar LAI to other treatments there are indications that another nutrient was limiting yield, possibly deficiencies in N or P. This is highlighted by the yield response seen from foliar N+K applications which gave a tolerance ratio greater than unity but had significantly lower ground cover at 66 DAP, similar ground cover and LAI at 108 to 110 DAP and a low LAI at 131 DAP, than all other foliar treatments in oxamyl untreated plots. The implication therefore, is that the addition of N to the foliar application of K rectified the potential deficiency and that K was not limiting. This observation is supported by Marschner (1995), who found that where N applications are made at apparently low levels of available K, a yield suppression and not a yield increase occurs, suggesting that K was not limiting. Where foliar P applications were made in non-oxamyl-treated plots a tolerance reduction occurred compared to the control plots without nematicide. The addition of foliar N to the foliar P application raised the tolerance level to that seen with the non oxamyl treated control but, unlike the N addition to foliar K, the tolerance ratio did not exceed unity. It could be suggested that the foliar P applications during the latter part of the season restricted yield improvements as any combination of applications which included foliar P reduced the tolerance levels found, and where it was applied alone, it significantly reduced the LAI at 131DAP. An important consideration, however, is that these experiments were carried out on soils with an ADAS P index of 5.0 for which there is a nil application recommendation. The use of a basal dressing of 100 kg P_2O_5/ha + 40 kg P_2O_5/ha as a foliar application may have increased the potential for early crop senescence. However, a yield increase would still be expected as Berryman *et al.*(1973) indicate that a yield benefit of approximately 1.3 t/ha does arise from additional P applications at a soil index of 4 or 5. The only benefit from foliar P came in the 66 DAP ground cover assessment, which is in line with the crop requirement at that stage of growth.

The lack of response from the applications of P and K may have come from a poor uptake of these nutrients through the leaves. Thus they may not have been deficient in the experiment or, if they were deficient and limiting yield, their application by this method failed to improve the tolerance of the plant. The nutrient sources were, however, chosen on the basis of known acceptability for foliar application as outlined by Bowen (1993), Barel and Black (1979) and Lewis and Kettlewell (1993).

3.6.9 Experiment considerations

The choice of the intolerant cultivar Pentland Dell was appropriate at the PCN population densities encountered in the experiments. These levels of PCN infestation, although high enough to cause some yield reduction, were not sufficient for there to be severe effects of PCN on the growth parameters measured. Further studies would therefore benefit from a higher PCN pressure both to clarify the effects and to assess the potential amelioration of the effects by subsequent fertiliser treatments.

The lack of scorch after applications of the foliar nutrients was probably due to the applications being made only in the evenings in suitable conditions. This would not normally be possible for large scale applications due to time constraints. The identification of appropriate concentrations and application timings are therefore essential if this method of increasing potato tolerance is to be developed. Urea-triazone solution can be applied at concentrations of 5.8-7.1% without leaf damage (Clapp, 1993) and may be a useful alternative to the straight urea used in these experiments.

The applications of the five foliar treatments in the experiments started at 54 and 56 DAP and they were completed by 93 and 110 DAP, for experiments one and two respectively. The actual timing of these applications may well have influenced the final yield of the treatments as Gunasena (1969) found that NPK uptake reaches a maximum at 128 DAP and Ezeta and McCollum (1972) that maximum daily uptake of N occurs between 95 and 137 DAP, and of K between 95 and 116 DAP, between which times the uptake rates were 2.5 kg N and 6.6 kg K per ha per day. If the applications of N were altered or extended to cover the maximum uptake period a greater tolerance benefit might be realised. The timing of the first foliar applications, 5-7 days before tuber initiation, is probably quite appropriate as a minimum ground cover for interception of the foliar application is required and the ground cover at that time was approximately 45%. At that time the plant is growing exponentially and any nutrient deficiencies could prevent the achievement of the good early ground cover required for high yields. The timing itself was based on the accumulated thermal time from planting as suggested by Jefferies and MacKerron (1987). The prediction of tuber initiation, TI, at 660 degree-days was fairly accurate for the cultivar Pentland Dell in this experiment as the actual onset of TI was recorded after 642 to 671 day degrees (23rd to 25th June, 57 to 59 DAP). The first foliar application at 54 DAP (20th June) was therefore about 3 days pre-TI and close to the planned 7 days pre-TI. Planning of this application based on day-degrees does, however, depend on a fairly accurate judgement of expected temperatures as accumulated thermal time for TI approaches. The requirement for this timing to be exact is debateable and, as long as the first application is made at approximately this time, day-degree accumulation may simply serve as a useful indicator.

The experimental design, i.e. split-plot randomised block, may not have been the most effective to distinguish the differences between the treatments. The design can, however, minimise variation in soil nutrient status and PCN populations where nematicide treatments and nutrients are being studied. A normal randomised block with one or two nematicide control treatments may, however, have been more useful in this type of experiment.

Monitoring of the site for soil moisture deficits showed that with a mean for the growing season of 28mm (only 22mm until later in the season) the moisture level of the soil should not have been restrictive to crop growth (Harris, 1992).

3.7 Conclusions

Although somewhat inappropriate experimental designs and low levels of PCN soil infestation have led to inconclusive results, the results have provided some useful information from which further investigations can be based. There was weak evidence to suggest that both haulm and root growth can be enhanced by foliar nutrient applications, and that this is most pronounced when the seedbed fertiliser is applied in the broadcast granular form. Improvements in the early percentage ground cover, along with reduced LAI later in the growing period and therefore yield, suggest that applications of foliar P may only be beneficial during the early stages of growth. The benefits to LAI and tuber yield from foliar N, however, suggest that this nutrient is also worthy of further investigation. Nutrient analysis of the plants showed that P concentration was the most affected by PCN infection but future experiments will have to use higher PCN population densities to make the effects clearer. The P deficit was redressed with both liquid placed fertiliser and applications of foliar PK, but this did not improve tuber yield. This suggests that the relationship between PCN and the plant is complex and that the effects on yield cannot be negated by the simple amelioration of the nutrient deficit. Further experimental field work will need to incorporate a more sensitive experiment design, higher PCN population densities, a more suitable nematicide incorporation method and earlier analysis of root invasion if more definitive results are to be obtained.

4. The 1997 field experiments

4.1 Introduction

The 1996 field experiments investigated two aspects of potato crop nutrition in the presence of PCN; these were I) whether basal fertiliser application method could influence both the tolerance of the plant and the response to foliar applications of N, P and K, and ii) whether single or combined applications of foliar N, P and K, in addition to a basal liquid placed fertiliser, could influence the tolerance of PCN infected plants in a set programme of applications. The basal fertiliser experiment (chapter 3) produced no significant benefits in potato yield from either basal fertiliser application method or from the application of foliar NPK. There was some evidence to suggest that liquid placed fertiliser increased the nutrient concentrations within the plants but the PCN-induced nutrient deficit remained constant. The experiment with individual or combined applications of foliar N, P and K showed evidence, in plots not treated with oxamyl, of benefits to early ground cover from foliar P; reduced LAI from foliar P and foliar N + P at 110 DAP; increased LAI from foliar N, at 131 DAP; and yields from applications of foliar N and foliar N + K similar to those in plots treated with oxamyl. The conclusions from that work were that the reduction of percentage ground cover and LAI associated with PCN (Trudgill *et al.*,1975a; Van Oijen *et al.*,1995) could be ameliorated if the foliar applications favoured P in the early growing period and N in the mid to late part of the growing period. As the known effects of N and P fertiliser applications, in the absence of PCN infection, are for P applications to increase LAI in the early stages of crop growth and N to increase it in the later stages of crop growth (Dyson & Watson, 1971; Harris, 1992), the foliar applications planned for the experiments described in this chapter would also still follow conventional fertiliser practices. The planned fertiliser applications would also explore the suggestions by Trudgill *et al.* (1975a) that N was not deficient before 11 weeks after planting, and Trudgill (1980) where the lower growth rate of PCN infected plants seemed to be due to reduced uptake of P and N.

The 1997 experiments were planned as field experiments, rather than glasshouse experiments, which Trudgill (1980) had shown to contradict field experiments. This made it possible to repeat and expand upon selected treatments from the 1996 work. In contrast to the 1996 experiments, which were made on a site where the *Globodera pallida* population density averaged 16 eggs/g soil, the 1997 experiments used a much higher PCN population density (average of 86 eggs/g soil) with both *G. pallida* and *G. rostochiensis* present. This level of infestation would cause more severe plant symptoms of PCN invasion and allow further investigation of both the symptoms and the ability of the foliar fertilisers to increase the plant's tolerance of PCN invasion. The cultivar Santė was chosen for the 1997 experiments because it is relatively tolerant of PCN attack (Whitehead *et al.*, 1991b; Haydock *et al*, 1996), so total crop loss would not occur. This would allow tolerance improvements to be seen and would also investigate the response to foliar nutrients of a different potato cultivar. Other aspects of the field experiments, i.e. soil type, irrigation, planting density and crop husbandry, were similar in both years.

4.1.1 Aims of the 1997 investigations

i) Experiment one

The first experiment was designed to investigate whether:

a) the early ground cover of PCN infected potato plants could be influenced by a single foliar P application at tuber initiation, using two rates of application;

b) applications of foliar N influence the effects of foliar P application on ground cover in PCN infected potato plants;

c) foliar N applications are beneficial to plant growth, crop yield and plant tolerance in four or five application regimes;

d) early foliar P application, with or without foliar N at the same time, would affect crop yield and plant tolerance when incorporated in a four or five foliar N application regime;

e) if any of the foliar applications affected PCN invasion or development;

f) foliar nutrient applications influenced the nutrient status of the PCN infected potato plant.

The title for the experiment was :

The growth and yield responses to supplementary foliar nitrogen and foliar phosphate of potatoes infected by potato cyst nematodes.

ii) Experiment two

A second experiment was designed to continue the investigation of the role of foliar nitrogen in improving the tolerance of PCN infected potato plants by investigating:

a) if rates of foliar N, applied at concentrations from zero to 6%, influenced the development of the plant, crop yield or PCN tolerance of the plant;

b) if any of the foliar applications affected PCN invasion or development;

c) the effects of the foliar nutrient applications on the nutrient status of the PCN infected potato plant.

The title for the experiment is :

The growth and yield responses to supplementary foliar nitrogen of potatoes infected by potato cyst nematodes.

iii) Experiment three

A final experiment was designed to investigate further the effects of the basal fertiliser practice on the PCN tolerance of the potato plant. The normal practice for the application of the crop requirements for nitrogen is to apply the whole quantity of N at planting unless planting on a light, free draining or well irrigated soil, when the application is split (Anon, 1994). This is to prevent leaching of the nutrient. However, applying all of the crop N requirement even on light soils at planting may improve the availability of this nutrient for a root system struggling to develop under PCN attack. Alternatively, splitting the crop N requirements between planting and tuber initiation application may improve the availability of N to a root system, reduced by PCN attack, later in the season. As the results of 1996 individual or combined applications of foliar N, P and K experiment suggested benefits to the tolerance of the crop by applications of foliar N, therefore, the 1997 experiments also incorporated this treatment. The aims of the experiment were to investigate whether:

a) the application of the recommended (Anon, 1994) level of nitrogen would be beneficial to plant growth, crop yield, nutrient status and tolerance of the crop when applied as 50/50, 66/33 or 100/0 % splits between planting and tuber initiation, when supplemented by a five foliar N applications;

b) foliar or seedbed nitrogen applications affected PCN invasion or development.

The title for this experiment was:

The growth and yield responses to basal, tuber initiation and supplementary foliar nitrogen of potatoes infected by potato cyst nematodes.

4.2 General material and methods

Three field experiments were located at a field site in Shropshire, grid reference SO775954, where the Blackwood series sandy loam soil (O.S., 1983) gave average ADAS nutrient indices (Anon, 1994) of N = 0, P = 4- (48 mg P/l), K = 2+ (193 mg K/l), Mg = 0, and pH = 7.1. The previous crop was sugar-beet and no organic manures had been applied in the previous five years. Kieserite (16-17% Mg) was applied at 101 kg/ha 12 days before planting. Primary cultivations: ploughed to 30 cm depth, shallow bed-formed; deep bed-forming and destoning were done on the day of planting. Each bed was split into two rows of 91.5 cm at planting. Nematicide treated plots received oxamyl as Vydate (10% oxamyl w/w, gr. Du Pont (UK)) at 5.5 kg a.i./ha applied by hand and incorporated by a Reekie reliance destoner. Chitted potato seed *(Solanum tuberosum)* cv. Santé, super elite grade 1, was planted on 9th April at 15-20 cm depth and 28-30 cm spacing (approximately 39,000 seed tubers/ha) with a tractor mounted Bamlett automatic potato planter. Inorganic fertilisers were applied, by hand, as described in the individual experiments. Soil moisture deficits were maintained at 30 mm by rain gun irrigation and were monitored using an Institute of Hydrology neutron probe. Throughout the growing season environmental conditions were recorded as listed in section 2.1. The crop was grown using standard agrochemical practices for a commercially grown potato crop, for the control of weeds and the disease 'late blight'. All plots were three beds (six rows) wide and eight metres long. Each plot contained a central bed (two rows) which was used for non-destructive assessments and final yield, a row at either side of the yield bed for destructive analysis assessments and two outer guard-only rows.

4.2.1 Specific to experiment one

The growth and yield responses to supplementary foliar nitrogen and foliar phosphate of potatoes infected by potato cyst nematodes.

The experimental design was a randomised complete block with five replicates. The treatments were designed as planned orthogonal contrasts (Pearce, 1992a, 1992b). Basal granular fertilisers were broadcast by hand onto shallow formed beds one day before planting. Nitrogen was applied at 120 kg N/ha as ammonium nitrate (Hydro ExtraN, 34.5% N); phosphates were applied at 100 kg P_2O_5/ha as triple super phosphate (43% P_2O_5 soluble in water); potassium was applied at 250 kg K_2O/ha as muriate of potash (60% K_2O soluble in water). Tuber initiation nitrogen as ammonium nitrate (Hydro ExtraN, 34.5% N) was broadcast by hand during tuber initiation, 64 DAP, at a rate of 120 kg N/ha. A five foliar spray programme began at 68 days after planting with 14 day intervals between applications (Table 4.1). Treatments requiring no foliar nutrient applications received foliar water applications. Where both foliar nitrogen and foliar phosphate applications were required a single mixture was applied. Treatments applied were as follows: 1, five sequential applications of foliar water; 2, a first application of foliar water followed by four sequential 4% nitrogen applications; 3, a first application of 1.7% phosphate followed by four sequential 4% nitrogen applications; 4, a first application of 3.4% phosphate followed by four sequential 4% nitrogen applications; 5, five sequential applications of 4% nitrogen; 6, a first application of 4% nitrogen and 1.7% phosphate followed by four sequential applications of 4% nitrogen; 7, a first application of 4% nitrogen and 3.4% phosphate followed by four sequential 4% nitrogen applications. The mean initial PCN population density was 91 eggs/g soil. PCN species were identified by isoelectric focusing as predominantly *G. rostochiensis* with some *G. pallida*,

Table 4.1. Foliar fertiliser and nematicide treatments in an investigation of the growth and yield response to supplementary foliar nitrogen and foliar phosphate of potatoes infected by potato cyst nematodes.

	individual foliar applications						
	nitrogen			phosphate			
treatment code	%	kg/ha	schedule (DAP)[a]	%	kg/ha	(DAP)[a]	nematicide used
Std + O[b]	0.0	0.0		0.0	0.0		oxamyl[c]
Std + FN4	4.0	12.0	82, 96, 110, 124	0.0	0.0		none
Std + FN4P1	4.0	12.0	82, 96, 110, 124	1.7	5.1	68	none
Std + FN4P2	4.0	12.0	82, 96, 110, 124	3.4	10.2	68	none
Std + FN5	4.0	12.0	68, 82, 96, 110, 124	0.0	0.0		none
Std + FN5P1	4.0	12.0	68, 82, 96, 110, 124	1.7	5.1	68	none
Std + FN5P2	4.0	12.0	68, 82, 96, 110, 124	3.4	10.2	68	none

[a] DAP = days after planting
[b] Std + O = standard seed-bed fertiliser (240 kg N/ha; 100 kg P_2O_5/ha; 250 kg K_2O/ha) plus oxamyl; Std = standard seed-bed fertiliser without nematicide; + FN4 = plus four applications of foliar N; FN5 = five applications of foliar N; P1 = foliar phosphate at 1.7%; P2 = foliar phosphate at 3.4%.
[c] Oxamyl as Vydate (10% a.i. w/w.; Du Pont) at 5.5 kg a.i./ha

4.2.2 Specific to experiment two

The growth and yield responses to supplementary foliar nitrogen of potatoes infected by potato cyst nematodes.

The experimental design was a randomised complete block with five replicates and was based on planned orthogonal contrasts, which included a nematicide treated control. This design allowed statistical analysis as either Anova or as rate response with an additional control. Basal granular fertilisers were broadcast by hand onto shallow formed beds one day before planting. Nitrogen was applied at 120 kg N/ha as ammonium nitrate (Hydro ExtraN, 34.5% N); phosphates were applied at 100 kg P_2O_5/ha as triple super phosphate, 43% P_2O_5 soluble in water); potassium was applied at 250 kg K_2O/ha as muriate of potash (60% K_2O soluble in water). Tuber initiation nitrogen as ammonium nitrate (Hydro ExtraN, 34.5% N) was broadcast by hand during tuber initiation, 64 DAP, at a rate of 120 kg N/ha. A five foliar spray programme was initiated at 68 days after planting with 14 day intervals between applications (Table 4.2).

Table 4.2. Foliar fertiliser and nematicide treatments in an investigation of the growth and yield response to supplementary foliar nitrogen, of potatoes infected by potato cyst nematodes

treatment code	individual foliar applications			nematicide used
	%N	kg N/ha	spray schedule (DAP) [a]	
Std + O [b]	0.0	0.0		oxamyl[c]
Std	0.0	0.0		none
Std + Fol 2% N	2.0	6.0	68, 82, 96, 110, 124	none
Std + Fol 4% N	4.0	12.0	68, 82, 96, 110, 124	none
Std + Fol 6% N	6.0	18.0	68, 82, 96, 110, 124	none

[a] DAP = days after planting
[b] Std + O = standard seed-bed fertiliser (240 kg N/ha; 100 kg P_2O_5/ha; 250 kg K_2O/ha) plus oxamyl; Std = standard seed-bed fertiliser only; + Fol % N = plus foliar N.
[c] Oxamyl as Vydate (10% a.i. w/w.; Du Pont) at 5.5 kg a.i./ha.

Treatments requiring no foliar nutrient applications received foliar water applications. Foliar treatments applied were as follows: 1, five sequential applications of foliar water; 2, five sequential applications of foliar water; 3, five sequential applications of 2% N; 4, five sequential applications of 4% N; 5, five sequential applications of 6% N. The mean initial PCN population density was 76 eggs/g soil. PCN species were identified by isoelectric focusing as predominantly *G. rostochiensis* with some *G. pallida*,

4.2.3 Specific to experiment three

The growth and yield responses to basal, tuber initiation and supplementary foliar nitrogen of potatoes infected by potato cyst nematodes.

The experimental design was a randomised complete block with five replicates. This design included a nematicide treated control which could be analysed statistically as either a standard Anova or Anova with an additional control. Basal granular fertilisers were broadcast by hand onto shallow formed beds one day before planting, of which N was applied as described and listed below; phosphates were applied at 100 kg P_2O_5/ha as triple super phosphate (43% P_2O_5 soluble in water); potassium was applied at 250 kg K_2O/ha as muriate of potash (60% K_2O soluble in water). Tuber initiation nitrogen as ammonium nitrate (Hydro ExtraN, 34.5% N) was broadcast by hand during tuber initiation, 64 DAP, as required by the treatment list (Table 4.3). A five foliar spray programme was initiated at 68 days after planting with 14 day intervals between applications (Table 4.3). Treatments requiring no foliar nutrient applications received foliar water applications. Treatments applied were as follows: 1, five sequential applications of foliar water, 120 kg N/ha applied at planting and 120 kg N/ha applied at tuber initiation as ammonium nitrate (Hydro ExtraN, 34.5% N); 2, five sequential applications of foliar water, 120 kg N/ha applied at planting and 120 kg N/ha applied at tuber initiation as ammonium nitrate (Hydro ExtraN, 34.5% N); 3, five sequential 4% nitrogen applications, 120 kg N/ha applied at planting and 120 kg N/ha applied at tuber initiation as ammonium nitrate (Hydro ExtraN, 34.5% N); 4, five sequential 4% nitrogen applications, 180 kg N/ha applied at planting and 60 kg N/ha applied at tuber initiation as ammonium nitrate (Hydro ExtraN, 34.5% N); 5, five sequential applications of 4% nitrogen, 240 kg N/ha applied at planting as ammonium nitrate (Hydro ExtraN, 34.5% N) and no N applications at tuber initiation. The mean initial PCN population density was 90 eggs/g soil. PCN species were identified by isoelectric focusing as predominantly *G. rostochiensis* with some *G. pallida*,

Table 4.3. Fertiliser nitrogen and nematicide treatments in an investigation of the growth and yield response to basal, tuber initiation and supplementary foliar nitrogen of potatoes infected by potato cyst nematodes.

	nitrogen applications					
	granular (kg N/ha)		individual foliar N			nematicide used
treatment code [a]	planting	TI [b]	%	kg/ha	spray schedule (DAP) [c]	
Std + O	120	120	0.0	0.0		oxamyl[d]
Std	120	120	0.0	0.0		none
Std + F	120	120	4.0	12.0	68, 82, 96, 110, 124	none
HIGH + F	180	60	4.0	12.0	68, 82, 96, 110, 124	none
ALL + F	240	0.0	4.0	12.0	68, 82, 96, 110, 124	none

[a] Std = standard fertiliser practice, HIGH = higher N rate at planting, ALL = all N applied at planting, +O = plus oxamyl, +F = plus foliar N.
[b] TI = tuber initiation
[c] DAP = days after planting
[d] Oxamyl as Vydate (10% a.i. w/w.; Du Pont) at 5.5 kg a.i./ha

4.3 Results of experiment one

The growth and yield responses to supplementary foliar nitrogen and foliar phosphate of potatoes infected by potato cyst nematodes.

4.3.1 PCN populations

The PCN populations recorded on this experimental area were identified by isoelectric focusing as a combination of mainly *G. rostochiensis* and a little G. *pallida*.

i) Initial population density

The initial PCN population densities, with a mean of 91 eggs/g soil, did not differ significantly between treatments. There was, however, considerable variation between the treatment means, ranging from 63 to 112 eggs/g soil, which was reflected by the CV of 34.7%, which showed the variability on the site (Table 4.4).

Table 4.4. Initial (Pi) and final (Pf) PCN population densities (eggs/g soil), Pf/Pi ratios and potato root invasion by PCN (juveniles/g root) at 61 DAP in an investigation of the growth and yield response to supplementary foliar N and foliar P, and oxamyl of potatoes infected by PCN.

treatment	Pi (eggs/g soil)	Pf (eggs/g soil)	Pf/Pi	root invasion (juveniles/g root)
Std + O [a]	91	3	0.03	190
Std + FN4	69	5	0.07	2650
Std + FN4P1	100	11	0.09	2280
Std + FN4P2	111	17	0.15	1940
Std + FN5	112	5	0.05	2450
Std + FN5P1	88	9	0.09	1870
Std + FN5P2	63	4	0.05	2020
mean	91	8	0.07	1914
significance (P =)	n.s.	n.s.	n.s.	<0.001
SED	19.8	6.7	0.053	436.0
d.f.	24	24	24	24
CV%	34.7	139.5	115.4	36

[a] see table 4.1

ii) Final population density

The final PCN population densities were not significantly affected by any foliar nutrient or oxamyl applications (Table 4.4). The population densities were considerably reduced within the experiment from an initial population density mean of 91 eggs/g soil down to only 8 eggs/g soil. This was the result of PCN resistance within the cultivar Santé which is reviewed in the discussion at the end of this chapter. There was considerable variation in Pf within the experiment, represented by a CV of 139.5%.

iii) Potato root invasion

Analysis of root samples, taken at 61 DAP, showed that the application of oxamyl had very significantly (P<0.001) reduced the number of juveniles found in the plant roots, from a mean of 2202 juveniles/g root in plots receiving no nematicide, down to 190 juveniles/g root (Table 4.4). The oxamyl application could therefore be said to have created a relatively PCN-free control treatment against which the other PCN infected plants and treatments could be compared.

iv) Pf/Pi ratios

The Pf/Pi ratio was not significantly affected by any of the foliar nutrient or oxamyl applications (Table 4.4). The mean Pf/Pi ratio of 0.07 shows that the initial population was severely reduced within this experiment.

4.3.2 Plant growth

i) Plant emergence

Plant emergence was measured on six dates from 33 to 49 DAP. At 33, 35, 37 and 40 DAP the percentage of plants emerged was significantly higher in plots which had been treated with oxamyl (P = 0.003, 0.007, <0.001 and 0.004 respectively) (Table 4.5).

Table 4.5. The percentage emergence of potato plants in an investigation of the growth and yield response to supplementary foliar N, foliar P, and oxamyl of potatoes infected by potato cyst nematodes.

	days after planting					
treatment	33	35	37	40	42	49
Std + O [a]	35.8	54.9	77.6	92.1	95.0	100
Std + FN4	22.2	39.0	60.3	82.1	89.4	100
Std + FN4P1	24.4	39.7	66.6	86.6	90.2	100
Std + FN4P2	22.8	36.9	58.6	80.9	90.2	100
Std + FN5	18.6	35.5	58.7	83.3	89.8	100
Std + FN5P1	18.6	34.0	55.3	78.9	85.8	100
Std + FN5P2	21.0	36.7	58.3	80.2	88.6	100
mean	23.4	39.5	62.2	83.4	89.9	
significance (P =)	0.003	0.007	<0.001	0.004	n.s.	
SED	3.87	5.03	4.12	3.10	3.17	
d.f.	24	24	24	24	24	
CV%	26.2	20.1	10.5	5.9	5.6	

[a] see table 4.1

No treatment nutrients had been applied by the time of the emergence assessments and, therefore, the significant differences between treatment FN4P1 and FN5P1 at 37 and 40 DAP cannot be attributed to the treatment. Two methods of statistical analysis were used to investigate this anomaly further: linear regression was used to identify possible relationships between the rate of plant emergence and Pi, Log_e Pi, root invasion and Log_e root invasion; covariance analysis was used to remove any underlying differences in PCN populations between plots. At 37 and 40 DAP, the linear regressions (results not shown) showed no relationship between Pi or log_e Pi and the rate of plant emergence. The root invasion variate showed no evidence of a relationship with emergence at 40 DAP but very strong evidence ($P = 0.005$) of a relationship at 37 DAP although the adjusted r^2 of only 0.19 suggested that very little of the variability had been accounted for by the relationship. The $\log_e$ root invasion showed strong correlations ($P<0.001$ at 37 DAP; $P = 0.007$ at 40 DAP) with the rate of plant emergence and the $\log_e$ root invasion variates but again the adjusted r^2 values of 0.39 and 0.17, respectively, showed that very little of the variability was accounted for. The requirements for a linear relationships under the conditions of covariance use (Pearce, Clarke & Dyke, 1988) were only satisfied when $\log_e$ of root invasion was used to measure nematode stress. When the $\log_e$ root invasion analysis of covariance was carried out, all significant differences were removed but very little difference was made to the actual values (results not shown). The conclusions must be that the difference in the rate of plant emergence between treatments FN4P1 and FN5P1 cannot be attributed to differences in PCN pressure.

ii) Percentage ground cover

The percentage ground cover, estimated on 10 dates throughout the growing period, was significantly ($P<0.001$) higher at 49, 56, 68, 76, 85, 93, 104 and 120 DAP and significantly ($P = 0.002$) lower at 146 DAP in plots which had been treated with oxamyl than in untreated plots (Tables 4.6a and 4.6b). The application of foliar nutrients, which began at 68 DAP, had no significant effect on ground cover at any time during the growing period until 146 DAP, when all foliar nutrient applications, except FN5P2, had significantly ($P = 0.029$) more ground cover than the oxamyl treated plots. In the plots not treated with oxamyl, the foliar nutrient treatments that included five foliar N applications had higher mean ground cover than those including four foliar N applications for the whole growing period (Table 4.6b).

Table 4.6a. The percentage ground cover of potato plants in an investigation of the growth and yield response to supplementary foliar N and foliar P, and oxamyl of potatoes infected by potato cyst nematodes.

	days after planting				
treatment	49	56	68	76 [a]	85
Std + O [b]	36.2	51.6	85.2	95.2	98.4
Std + FN4	20.0	29.0	53.4	59.4	60.8
Std + FN4P1	23.0	29.6	54.4	59.8	63.4
Std + FN4P2	21.0	30.6	48.2	54.8	56.8
Std + FN5	22.0	30.0	52.4	58.4	62.8
Std + FN5P1	20.0	29.6	52.0	59.2	63.2
Std + FN5P2	20.8	30.8	56.4	61.4	67.2
mean	23.3	33.0	57.4	64.0	67.5
overall SED	1.98	2.39	4.16	3.32	4.92
d.f.	24	24	24	24	24
CV%	13.4	11.4	11.5	8.2	11.5
<u>significance (P =)</u>					
treatments	<0.001	<0.001	<0.001	<0.001	<0.001
oxamyl vs non oxamyl	<0.001	<0.001	<0.001	<0.001	<0.001
FN4 vs FN5	n.s.	n.s.	n.s.	n.s.	n.s.
no P vs mean P1 & P2	n.s.	n.s.	n.s.	n.s.	n.s.
P1 vs P2	n.s.	n.s.	n.s.	n.s.	n.s.
(FN4 vs FN5)*(No P vs P)	n.s.	n.s.	n.s.	n.s.	n.s.
(FN4 vs FN5)*(P1 vs P2)	n.s.	n.s.	n.s.	n.s.	n.s.

[a] 12 days after first foliar nutrient applications

[b] see table 4.1.

Table 4.6b. The percentage ground cover of potato plants in an investigation of the growth and yield response to supplementary foliar N and foliar P, and oxamyl of potatoes infected by potato cyst nematodes.

treatment	days after planting 93	104	120	133	146	season mean
Std + O [a]	99.0	99.0	90.4	38.4	3.4	69.7
Std + FN4	57.8	56.4	53.4	35.4	11.2	43.7
Std + FN4P1	59.2	62.2	58.6	35.2	11.6	45.7
Std + FN4P2	52.8	57.2	54.4	32.6	10.8	41.9
Std + FN5	59.6	62.0	60.8	41.2	13.6	46.3
Std + FN5P1	63.4	66.6	62.6	43.4	12.4	47.2
Std + FN5P2	64.0	68.2	62.0	33.8	7.8	47.2
mean	65.1	67.4	63.2	37.1	10.1	48.8
overall SED	5.73	6.57	5.58	5.23	2.88	3.33
d.f.	24	24	24	24	24	24
CV%	13.9	15.4	14.0	22.3	45.0	10.8
<u>significance (*P* =)</u>						
treatments	<0.001	<0.001	<0.001	n.s.	0.029	<0.001
oxamyl vs non oxamyl	<0.001	<0.001	<0.001	n.s.	0.002	<0.001
FN4 vs FN5	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
no P vs mean P1 & P2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
P1 vs P2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
(FN4 vs FN5)*(No P vs P)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
(FN4 vs FN5)*(P1 vs P2)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

[a] see table 4.1.

<u>iii) Plant fresh and dry weight</u>

Whole plants were removed from plots at 61 DAP, before the application of foliar nutrients. Both fresh and dry weights were significantly ($P<0.001$) greater where plants came from plots treated with oxamyl. There were no significant differences between the weights of plants from plots not treated with oxamyl, suggesting that, as no foliar applications had been applied at this time, these plants were comparable (Table 4.7).

Table 4.7. Fresh and dry weights of potato plants, 61 DAP, in an investigation of the growth and yield response to supplementary foliar N and foliar P, and oxamyl of potatoes infected by potato cyst nematodes.

	fresh weight (g)		dry weight (g)	
treatment	$\log_e$	back-trans [a]	$\log_e$	back-trans
Std + O [b]	6.183	484	3.616	37.2
Std + FN4	5.032	153	2.649	14.1
Std + FN4P1	5.107	165	2.709	15.0
Std + FN4P2	4.929	138	2.559	12.9
Std + FN5	4.978	145	2.613	13.6
Std + FN5P1	5.296	199	2.941	18.9
Std + FN5P2	5.146	172	2.756	15.7
mean	5.239		2.835	
overall SED	0.1744		0.1766	
d.f.	24		24	
CV%	5.3		9.9	
significance (P =)				
treatments	<0.001		<0.001	
oxamyl vs non oxamyl	<0.001		<0.001	
FN4 vs FN5	n.s.		n.s.	
no P vs mean P1 & P2	n.s.		n.s.	
P1 vs P2	n.s.		n.s.	
(FN4 vs FN5)*(No P vs P)	n.s.		n.s.	
(FN4 vs FN5)*(P1 vs P2)	n.s.		n.s.	

[a] back-trans = Log_e mean values back-transformed to indicate real values
[b] see table 4.1.

Table 4.8. The leaf discolouration of potato leaves at 98 DAP in an investigation of the growth and yield response to supplementary foliar N and foliar P, and oxamyl of potatoes infected by potato cyst nematodes.

treatment	discolouration % arctrans	discolouration % back-trans
Std + O [a]	1.81	0.1
Std + FN4	19.16	10.8
Std + FN4P1	12.99	5.1
Std + FN4P2	6.26	1.2
Std + FN5	18.56	10.1
Std + FN5P1	16.23	7.8
Std + FN5P2	9.21	2.6
mean	12.03	
overall SED	2.323	
d.f.	24	
CV%	30.5	
<u>significance (*P* =)</u>		
treatments	<0.001	
oxamyl vs non oxamyl	<0.001	
FN4 vs FN5	n.s.	
no P vs mean P1 & P2	<0.001	
P1 vs P2	<0.001	
(FN4 vs FN5)*(No P vs P)	n.s.	
(FN4 vs FN5)*(P1 vs P2)	n.s.	

[a] see table 4.1.

iv) Leaf discolouration

At 98 DAP plants were showing a severe brown 'speckling' discolouration of the leaves which initial observations suggested were treatment related. Plants in plots treated with oxamyl showed significantly (P<0.001) fewer areas of discolouration than those in untreated plots.

Where foliar applications had not included foliar P the discolouration was significantly (P<0.001) more pronounced than where foliar applications had included P. Further to this, where the foliar application of P was at the higher rate (P2) there was significantly (P<0.001) less discolouration than at the lower rate of P (P1) (Table 4.8).

4.3.3 Tuber yield and quality

The tuber yields, measured at 147 DAP, were significantly (P<0.001) increased in all grades where plots had been treated with oxamyl. In plots not treated with oxamyl; applying foliar N alone in four applications (FN4) did not improve or adversely affect the yield compared to applying five N applications (Table 4.9). When the four N applications were preceded by the low rate of foliar P (FN4P1) a 5 t/ha yield improvement was achieved over that with the four N applications alone but, the highest yield was achieved (29.5 t/ha) when the highest rate of foliar P (FN5P2) was included with the first of the five N applications (Table 4.9). None of these yield improvements were significant. The highest yield in plots not treated with oxamyl, 29.5 t/ha, from the application of five foliar N sprays with a high rate of early P, was 24.2 t/ha lower than the oxamyl treated yield (Table 4.9).

i) Effect of covariance on yield

The total tuber yield was analysed by covariance analysis to remove differences in initial PCN population (Pi) between plots, root invasion at 61 DAP and differences in the $\log_e$ transformed values of root invasion at 61 DAP. The yield in oxamyl treated plots remained significantly (P<0.001) higher than all the yields in plots not treated with oxamyl where the Pi and untransformed invasion covariates were used. Where the $\log_e$ of root invasion was used all yields became very similar and the increase in yield from oxamyl treated plots became non-significant (Table 4.10).

Table 4.9. Potato tuber yield (t/ha) at harvest (147 DAP) in an investigation of the growth and yield response to supplementary foliar N and foliar P, and oxamyl of potatoes infected by potato cyst nematodes.

	size grade (mm)					
treatment	<40	40-60	60-80	>80	ware	total
Std + O [a]	2.88	31.9	19.3	0.00	51.2	54.1
Std + FN4	1.89	13.2	8.4	0.07	21.6	23.5
Std + FN4P1	1.33	14.6	12.5	0.13	27.3	28.6
Std + FN4P2	1.45	12.7	7.9	0.00	20.7	22.1
Std + FN5	1.28	12.8	9.8	0.11	22.7	23.9
Std + FN5P1	1.28	12.9	1.08	0.58	24.3	25.5
Std + FN5P2	1.50	15.1	12.8	0.18	28.0	29.5
mean	1.66	16.2	11.7	n.a.[b]	28.0	29.6
overall SED	0.218	1.63	2.80	n.a.	4.12	4.07
d.f.	24	24	24	n.a.	24	24
CV%	20.8	16.0	38.0	n.a.	23.3	21.8
<u>significance (*P* =)</u>						
treatments	<0.001	<0.001	0.009	n.a.	<0.001	<0.001
oxamyl vs non oxamyl	<0.001	<0.001	<0.001	n.a.	<0.001	<0.001
FN4 vs FN5	n.s.	n.s.	n.s.	n.a.	n.s.	n.s.
no P vs mean P1 & P2	n.s.	n.s.	n.s.	n.a.	n.s.	n.s.
P1 vs P2	n.s.	n.s.	n.s.	n.a.	n.s.	n.s.
(FN4 vs FN5)*(No P vs P)	0.029	n.s.	n.s.	n.a.	n.s.	n.s.
(FN4 vs FN5)*(P1 vs P2)	n.s.	n.s.	n.s.	n.a.	n.s.	n.s.

[a] see table 4.1.
[b] n.a. analysis not applicable (too few values)

When tuber yields were analysed with invasion and $\log_e$ invasion covariates, however, a significant interaction was shown between the use of a four or five N application regime and the addition of either a low or high rate of early phosphate. The invasion covariate analysis showed that the yields of the four N applications with the low rate of early P (30.7 t/ha) or the five N application with the high rate of early foliar P (30.1 t/ha), were significantly ($P = 0.009$) higher than when the four foliar N was accompanied by the high rate of foliar P (22.3 t/ha) or when the five foliar N application included the low rate of foliar P (25.3 t/ha). The trend was exactly the same with the $\log_e$ root invasion covariate, but the values were slightly higher (Table 4.10).

ii) PCN relationship to total crop yield

Where there is underlying variation within an experimental site that cannot be controlled by the practice of 'blocking' an experiment, it is useful to use covariate analysis to remove this source of variation. There are rules regarding the suitability of variables for use as covariates which should be checked before their use: the variable in question must not be affected by the treatments; the covariate must be measurable quantitatively; and there must be a linear relationship between the two variables being studied (Gomez & Gomez, 1984). When the variable chosen as a covariate is analysed alone there is no requirement that it is significantly affected by the treatments. Thus the use of Pi as a covariate is unacceptable because the treatment with oxamyl, within the experiment, effectively negates the Pi value. The invasion of potato roots by PCN juveniles is, however, potentially more suited as a covariate as it is a quantitative expression of the actual PCN pressure which exists within the experiment.

a) Simple linear relationship

No significant relationship was found between Pi and total crop yield; the adjusted r^2 was only 0.02. However, there were significant ($P<0.001$) linear relationships of both root invasion and $\log_e$ root invasion with total yield (Figure 4.1 and 4.2), with r^2 values of 0.64 and 0.77 respectively. This suggests that root invasion or $\log_e$ root invasion are more suited as covariates in this experiment. When the values from oxamyl treated plots were removed from the regression (results not shown) Pi, root invasion and $\log_e$ root invasion would all equally be suitable as covariates.

Table 4.10. Effect of covariance on the analysis of potato total tuber yields (t/ha) in an investigation of the growth and yield response to supplementary foliar N and foliar P, and oxamyl of potatoes infected by potato cyst nematodes.

treatment	covariance type			
	none	Pi [a]	invasion [b]	$\log_e$ invasion [c]
Std + O [d]	54.1	54.1	44.1	32.1
Std + FN4	23.5	21.5	27.8	29.0
Std + FN4P1	28.6	29.5	30.7	32.9
Std + FN4P2	22.1	24.1	22.3	24.3
Std + FN5	23.9	26.0	27.1	29.1
Std + FN5P1	25.5	25.3	25.3	27.6
Std + FN5P2	29.5	26.8	30.1	32.5
mean	29.6	29.6	29.6	29.6
overall SED	4.07	3.81	3.70	5.78
d.f.	24	24	24	24
CV%	21.8	19.6	17.4	18.8
<u>significance (*P* =)</u>				
covariance	n.a.	0.017	<0.001	0.006
treatments	<0.001	<0.001	0.001	n.s.
oxamyl vs non oxamyl	<0.001	<0.001	<0.001	n.s
FN4 vs FN5	n.s.	n.s.	n.s.	n.s.
no P vs mean P1 & P2	n.s.	n.s.	n.s.	n.s.
P1 vs P2	n.s.	n.s.	n.s.	n.s.
(FN4 vs FN5)*(No P vs P)	n.s	n.s.	n.s.	n.s.
(FN4 vs FN5)*(P1 vs P2)	n.s.	n.s.	0.009	0.014.

[a] Initial PCN population
[b] PCN invasion of roots (juveniles/g root) 61 days after planting.
[c] $\log_e$ transformed values of PCN invasion of roots (juveniles/g root) 61 days after planting
[d] see table 4.1.

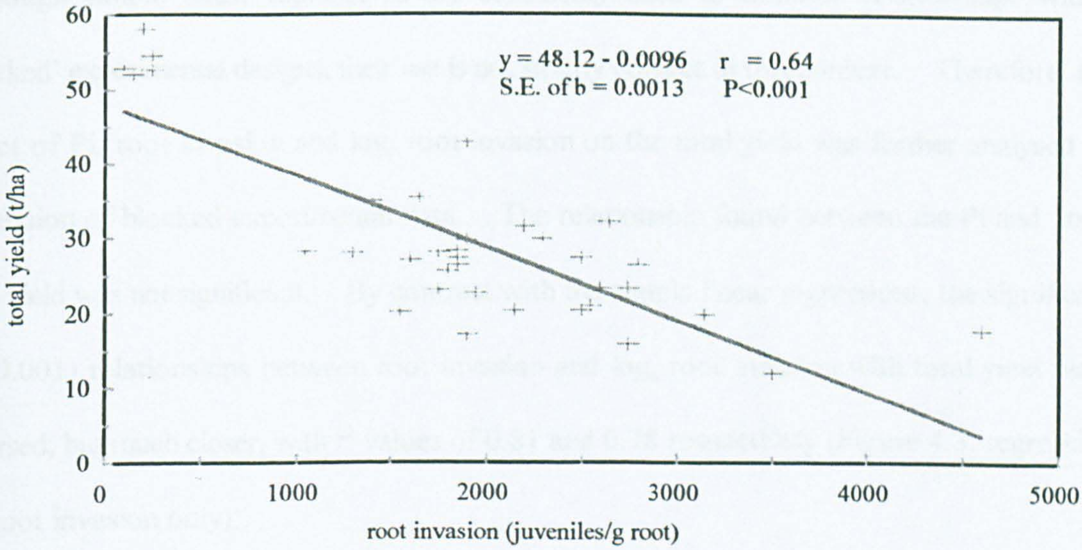

Figure 4.1. The simple linear relationship between PCN root invasion and total potato yield at harvest (147 DAP) in an investigation of the growth and yield response to supplementary foliar N and foliar P, and oxamyl of potatoes infected by potato cyst nematodes.

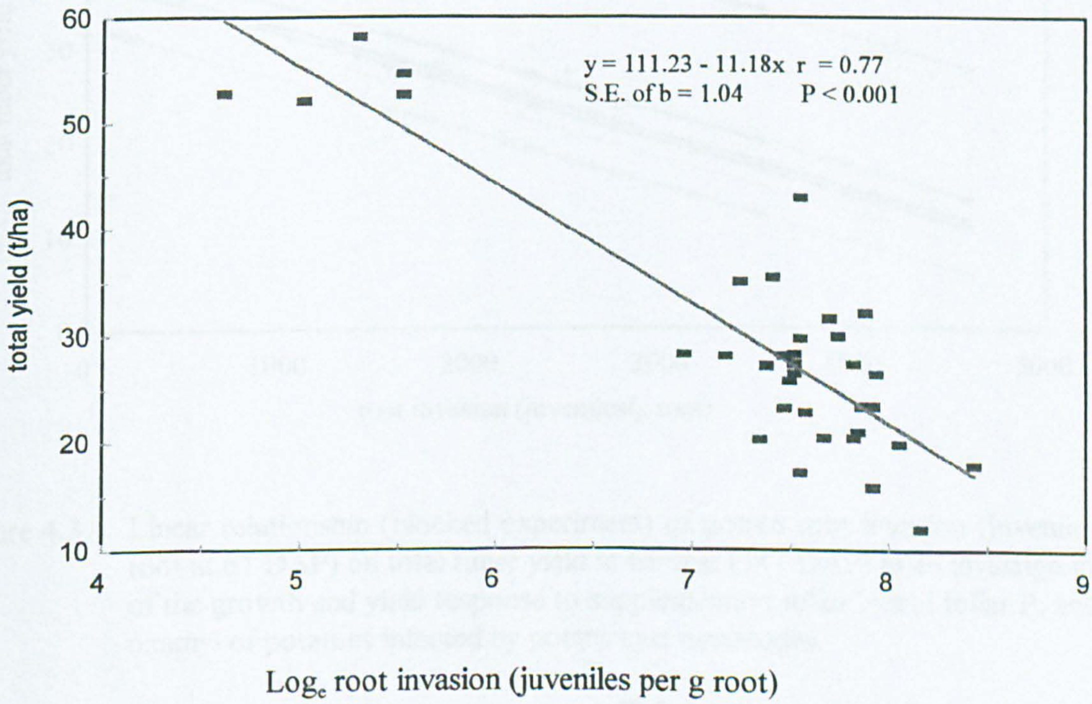

Figure 4.2. The simple linear relationship between $\log_e$ root invasion and total potato yield at harvest (147 DAP) in an investigation of the growth and yield response to supplementary foliar N and foliar P, and oxamyl of potatoes infected by potato cyst nematodes.

b) Regression of yield on blocked experimental data

Although simple linear regressions are commonly used to describe relationships within 'blocked' experimental designs, their use is not strictly correct in this context. Therefore, the effect of Pi, root invasion and $\log_e$ root invasion on the total yield was further analysed by regression of blocked experimental data. The relationship found between the Pi and total crop yield was not significant. By contrast with the simple linear regressions, the significant (P<0.001) relationships between root invasion and $\log_e$ root invasion with total yield were reversed, but much closer, with r^2 values of 0.81 and 0.78 respectively (Figure 4.3, regression for root invasion only).

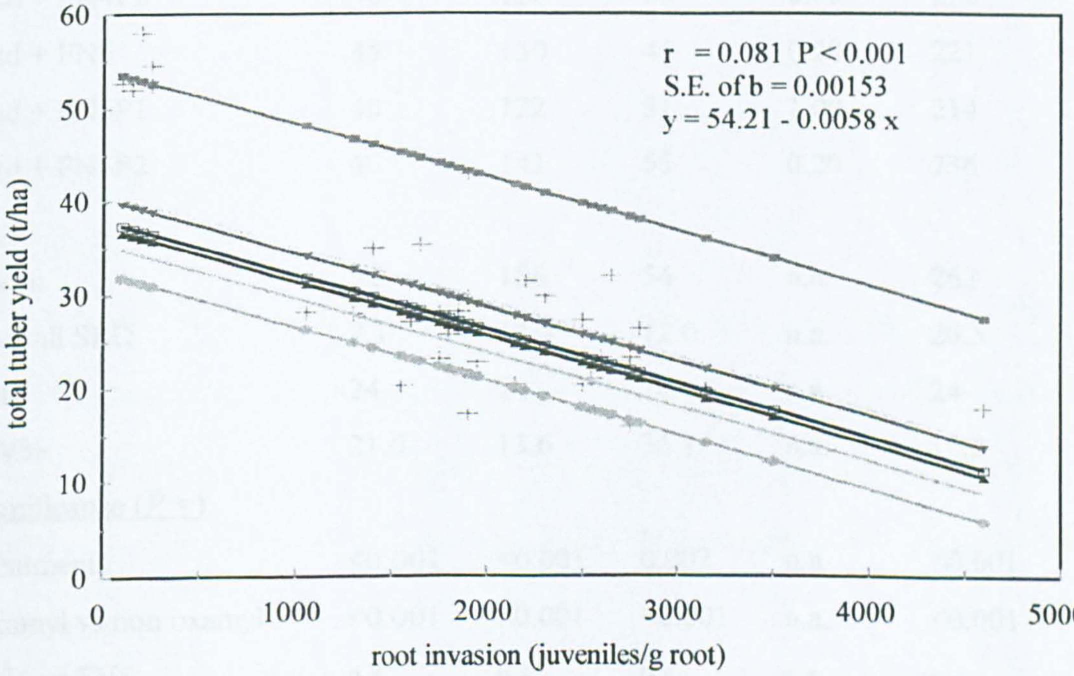

Figure 4.3. Linear relationship (blocked experiment) of potato root invasion (juveniles/g root at 61 DAP) on total tuber yield at harvest (147 DAP) in an investigation of the growth and yield response to supplementary foliar N and foliar P, and oxamyl of potatoes infected by potato cyst nematodes.

[a] Regression line parameters : ■ Std + O y = 54.21 - 0.0058x;
□ Std + FN4 y = 37.96 - 0.0058x; ⊠ Std + FN4P1 y = 40.88 - 0.0058x
● Std + FN4P2 y = 32.41 - 0.0058x; ▲ Std + FN5 y = 37.23 - 0.0058x
+ Std + FN5P1 y = 35.44 - 0.0058x; ▼ Std + FN5P2 y = 40.27 - 0.0058x

The absence of a linear relationship between Pi and yield and the clear relationship between root invasion and $\log_e$ root invasion on total yield, suggests that the latter two variables are more suited as covariates in the analysis of total yield (section 4.3.3.i).

Table 4.11. Numbers of potato tubers per plot at harvest (147 DAP) in an investigation of the growth and yield response to supplementary foliar N and foliar P, and oxamyl of potatoes infected by potato cyst nematodes.

	size grade (mm)				
treatment	<40	40-60	60-80	>80	total
Std + O [a]	91	304	93	0.00	489
Std + FN4	55	132	40	0.20	228
Std + FN4P1	45	134	57	0.20	235
Std + FN4P2	46	128	36	0.00	210
Std + FN5	45	130	45	0.20	221
Std + FN5P1	40	122	51	1.00	214
Std + FN5P2	40	141	55	0.20	236
mean	52	156	54	n.a.	262
overall SED	7.1	13.4	12.0	n.a.	20.5
d.f.	24	24	24	n.a.	24
CV%	21.6	13.6	35.1	n.a.	12.3
<u>significance (*P* =)</u>					
treatments	<0.001	<0.001	0.002	n.a.	<0.001
oxamyl vs non oxamyl	<0.001	<0.001	<0.001	n.a.	<0.001
FN4 vs FN5	n.s.	n.s.	n.s.	n.a.	n.s.
no P vs mean P1 & P2	n.s.	n.s.	n.s.	n.a.	n.s.
P1 vs P2	n.s.	n.s.	n.s.	n.a.	n.s.
(FN4 vs FN5)*(No P vs P)	n.s	n.s.	n.s.	n.a.	n.s.
(FN4 vs FN5)*(P1 vs P2)	n.s.	n.s.	n.s.	n.a.	n.s.

[a] see table 4.1.

[b] n.a. analysis not applicable (too few values)

iii) Tuber number

The application of oxamyl to plots significantly ($P<0.001$) increased the number of tubers in all grades and, overall, produced double the number of tubers found in all plots not treated with oxamyl. In plots not treated with oxamyl, the five foliar nitrogen regimes which included foliar phosphate produced significantly ($P<0.001$) less tubers in the <40mm grade than all other foliar nutrient treatments. There were no other significant differences (Table 4.11).

iv) Tuber dry matter

The percentage tuber dry matter, measured one day after harvest (148 DAP), was shown to be significantly ($P = 0.005$) higher with tubers from plots treated with oxamyl. The application of foliar nutrients had no significant effect (Table 4.12).

4.3.4 Nutrient status

i) Whole plant at 61 DAP

The percentage of N, P and K measured in whole plant dry matter was significantly ($P<0.001$) higher in plants from plots treated with oxamyl. The absence of significant differences between plants from treatments allocated to plots not treated with oxamyl demonstrates their overall similarity at this time, seven days before the commencement of foliar nutrient applications.

ii) Fourth leaf at 104 DAP

The percentage N and P in the fourth leaf (including petiole) dry matter was significantly ($P<0.001$) lower where leaves came from plots treated with oxamyl. There were no significant differences in percentage N or P attributable to foliar nutrient applications. There were no significant differences in K content of leaves between any treatments (Table 4.13).

Table 4.12. Percentage tuber dry matter at harvest (147 DAP) in an investigation of the growth and yield response to supplementary foliar N and foliar P, and oxamyl of potatoes infected by potato cyst nematodes.

treatment	dry matter %
Std + O [a]	21.80
Std + FN4	20.75
Std + FN4P1	21.05
Std + FN4P2	20.65
Std + FN5	20.40
Std + FN5P1	20.65
Std + FN5P2	21.00
mean	20.90
overall SED	0.449
d.f.	24
CV%	3.4
<u>significance (P =)</u>	
treatments	0.098
oxamyl vs non oxamyl	0.005
FN4 vs FN5	n.s.
no P vs mean P1 & P2	n.s.
P1 vs P2	n.s.
(FN4 vs FN5)*(No P vs P)	n.s.
(FN4 vs FN5)*(P1 vs P2)	n.s.

[a] see table 4.1.

Table 4.13. Nutrient concentrations of whole potato plant dry matter, at 61 DAP, and potato fourth leaf plus petiole at 104 DAP, in an investigation of the growth and yield response to supplementary foliar N and foliar P, and oxamyl of potatoes infected by potato cyst nematodes.

	61 DAP			104 DAP		
treatment	%N	%P	%K	%N	%P	%K
Std + O [a]	3.54	0.324	6.93	3.23	0.125	4.69
Std + FN4	3.18	0.253	5.46	3.85	0.153	4.69
Std + FN4P1	3.10	0.236	5.26	3.81	0.156	4.72
Std + FN4P2	3.16	0.246	5.49	3.78	0.161	4.77
Std + FN5	3.18	0.246	5.22	3.89	0.163	4.61
Std + FN5P1	3.26	0.241	5.57	3.90	0.153	4.56
Std + FN5P2	3.10	0.238	5.38	3.82	0.146	4.66
mean	3.22	0.255	5.62	3.75	0.151	4.67
overall SED	0.100	0.0130	0.235	0.094	0.0092	0.175
d.f.	24	24	24	24	24	24
CV%	4.9	8.1	6.6	4.0	9.6	5.9
<u>significance (*P* =)</u>						
treatments	0.003	<0.001	<0.001	<0.001	0.008	n.s.
oxamyl vs non oxamyl	<0.001	<0.001	<0.001	<0.001	<0.001	n.s.
FN4 vs FN5	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
no P vs mean P1 & P2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
P1 vs P2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
(FN4 vs FN5)*(No P vs P)	n.s	n.s.	n.s.	n.s.	n.s.	n.s.
(FN4 vs FN5)*(P1 vs P2)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

[a] see table 4.1.

iii) PCN effect on nutrient status

a) Simple linear relationship

The initial PCN population, Pi, was not related to the N, P or K concentration in the whole plant dry matter at 61 DAP. The number of PCN juveniles counted in the plant roots at 61

DAP showed some relationship to the N status of the plant ($P = 0.007$) but the adjusted r^2 was only 0.18. With increasing numbers of PCN juveniles in the roots, P and K concentrations decreased significantly ($P<0.001$) with r^2 values of 0.49 for P and 0.68 for K, suggesting that both P and K concentrations in potato plants are affected by root invasion by PCN (Figures 4.4 and 4.5).

b) Blocked experiment relationship

There were no significant blocked relationships between Pi and the N, P or K concentration of plants, but analysis of the root invasion data with blocked regression showed pronounced root invasion effects on the N, P and K concentrations of whole plant dry matter at 61 DAP. Root invasion significantly ($P = 0.002$) reduced the N concentration and an adjusted r^2 of 0.50 shows that much more of the variance was explained with this analysis than with the simple regression. Root invasion also significantly ($P<0.001$) reduced the P and K concentrations with adjusted r^2 values of 0.66 and 0.73 respectively.

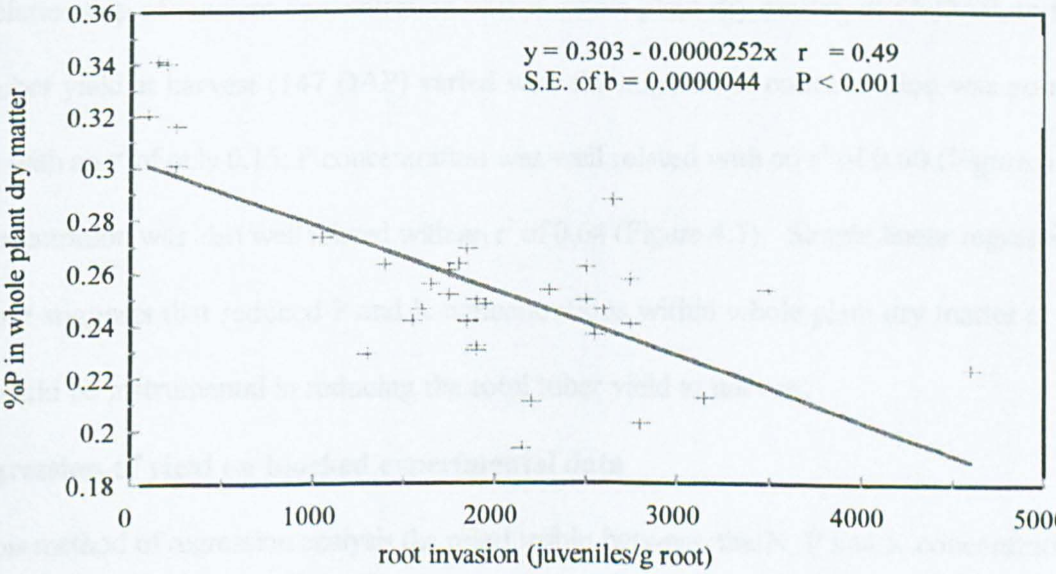

Figure 4.4. The simple linear relationship between PCN root invasion at 61 DAP and %P measured in whole plant dry matter in an investigation of the growth and yield response to supplementary foliar N and foliar P, and oxamyl of potatoes infected by potato cyst nematodes.

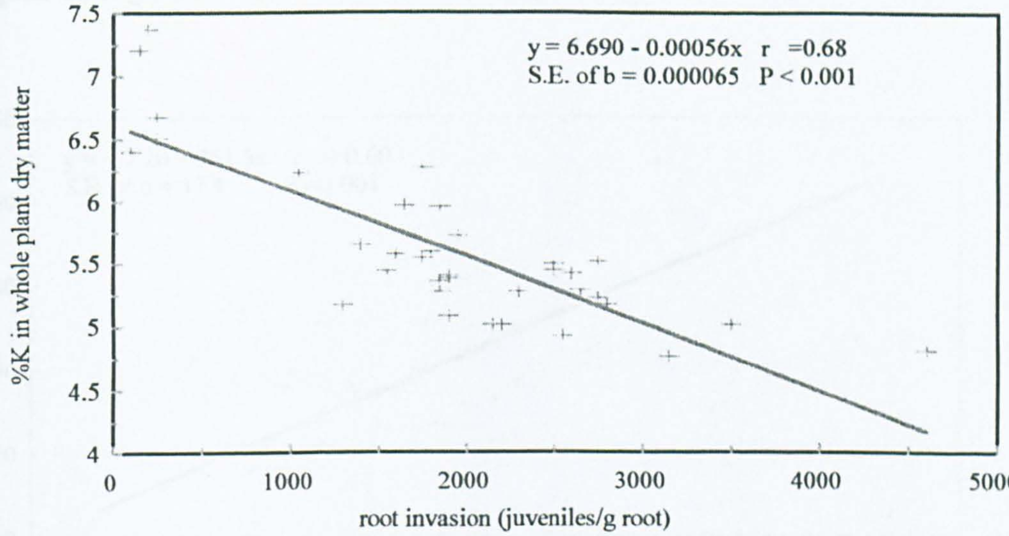

Figure 4.5. The simple linear relationship between PCN root invasion at 61 DAP and %K measured in whole plant dry matter in an investigation of the growth and yield response to supplementary foliar N and foliar P, and oxamyl of potatoes infected by potato cyst nematodes.

iv) Relationship between plant nutrient contents and tuber yield

a) Simple linear relationship

The relationship of nutrient concentration within whole plant dry matter, at 61 DAP, to the total tuber yield at harvest (147 DAP) varied with the nutrient; N concentration was poorly related with an r^2 of only 0.15; P concentration was well related with an r^2 of 0.60 (Figure 4.6) ; K concentration was also well related with an r^2 of 0.64 (Figure 4.7). Simple linear regression therefore suggests that reduced P and K concentrations within whole plant dry matter at 61 DAP could be instrumental in reducing the total tuber yield at harvest.

b) Regression of yield on blocked experimental data

With this method of regression analysis the relationship between the N, P and K concentration within whole plant dry matter at 61 DAP and total tuber yield at harvest (147 DAP) showed a closer association. N concentration was closely related to yield with an adjusted r^2 of 0.70, and the values for P and K concentration were 0.74 and 0.78 respectively (Figure 4.8, regression for K only). This method of analysis suggests that lower concentrations of N, P and

K were quite strongly correlated with lower tuber yields.

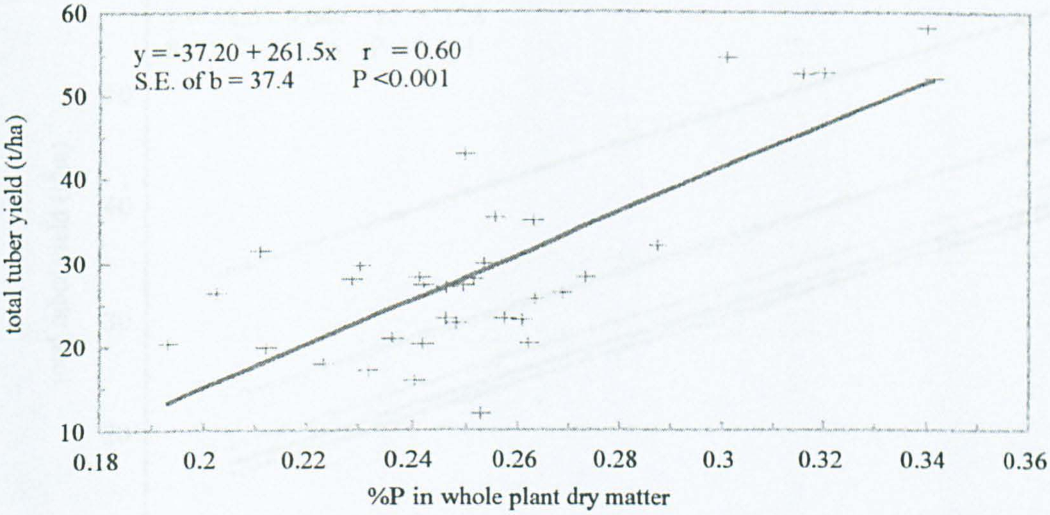

Figure 4.6. The simple linear relationship of P concentration in whole plant dry matter at 61 DAP on the total tuber yield at harvest (147 DAP) in an investigation of the growth and yield response to supplementary foliar N and foliar P, and oxamyl of potatoes infected by potato cyst nematodes.

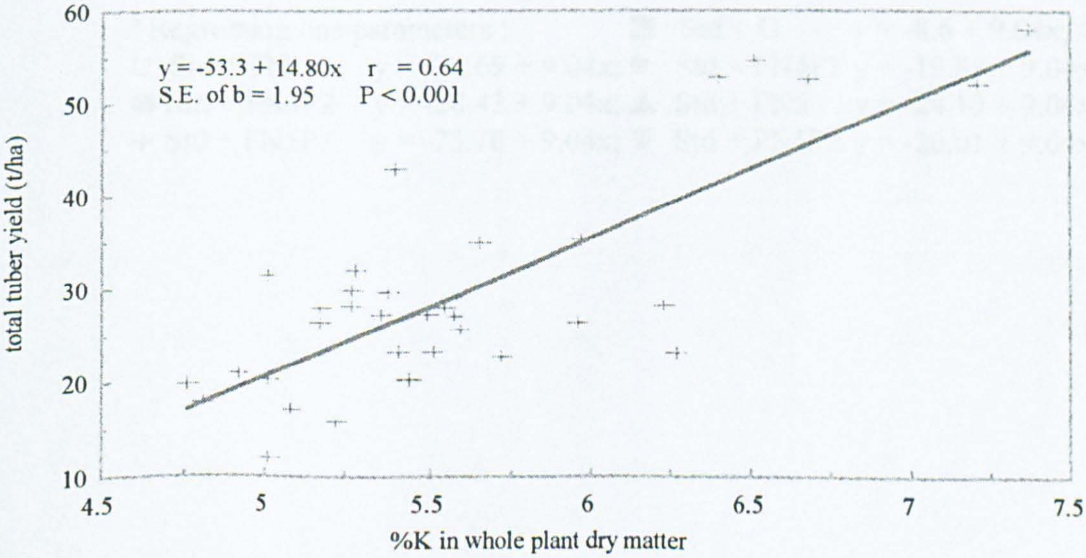

Figure 4.7. The simple linear relationship of K concentration in whole plant dry matter at 61 DAP on total tuber yield at harvest (147 DAP) in an investigation of the growth and yield response to supplementary foliar N and foliar P, and oxamyl of potatoes infected by potato cyst nematode.

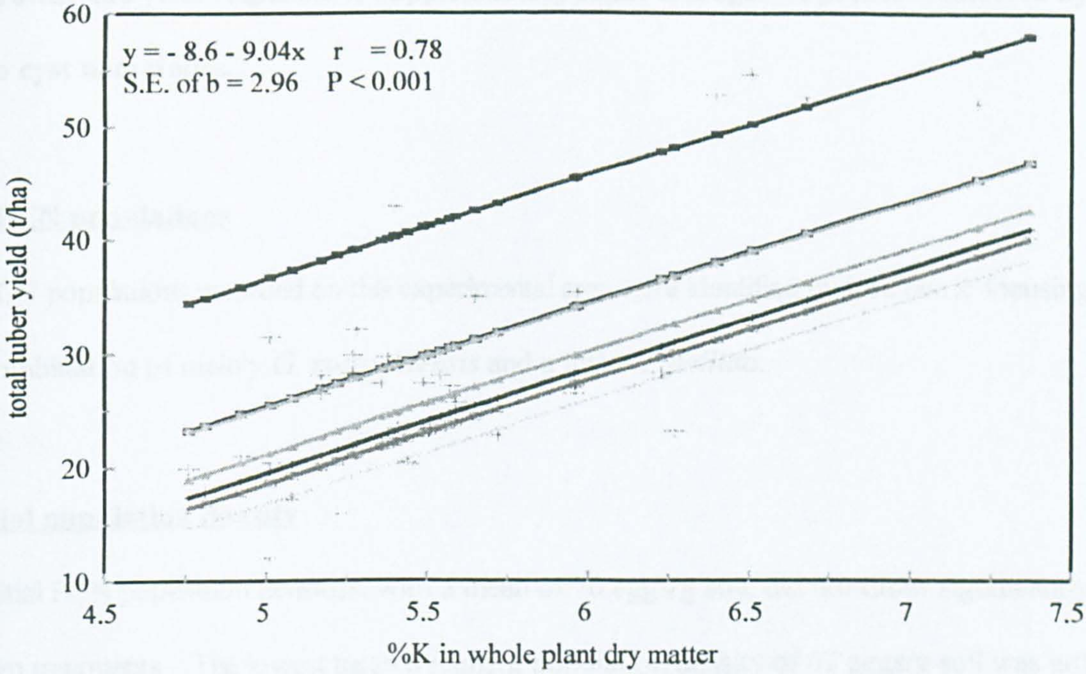

Figure 4.8. Blocked experiment relationship of K concentration in whole plant dry matter at 61 DAP on the total tuber yield at harvest (147 DAP) in an investigation of the growth and yield response to supplementary foliar N, foliar P and oxamyl, of potatoes infected by potato cyst nematodes.

[a] Regression line parameters : ■ Std + O $y = -8.6 + 9.04x$;
□ Std + FN4 $y = -26.69 + 9.04x$; ⊠ Std + FN4P1 $y = -19.85 + 9.04x$
● Std + FN4P2 $y = -28.43 + 9.04x$; ▲ Std + FN5 $y = -24.10 + 9.04x$
+ Std + FN5P1 $y = -25.70 + 9.04x$; ▼ Std + FN5P2 $y = -20.01 + 9.04x$

4.4 Results of experiment two

The growth and yield responses to supplementary foliar nitrogen of potatoes infected by potato cyst nematodes.

4.4.1 PCN populations

The PCN populations recorded on this experimental area were identified by isoelectric focusing as a combination of mainly *G. rostochiensis* and a little G. *pallida*.

i) Initial population density

The initial PCN population densities, with a mean of 76 eggs/g soil, did not differ significantly between treatments. The lowest mean treatment population density of 62 eggs/g soil was not greatly different to the highest population density of 85 eggs/g soil but the CV of 32.3% reflects the variability across the site (Table 4.14).

ii) Final population density

The final PCN population densities were not significantly affected by any of the treatments (Table 4.14). The final population densities were considerably reduced from the initial population density mean of 76 eggs/g soil-down to only 7 eggs/g soil. Despite the closeness of the means, there was considerable variation within the experiment represented by a CV of 92.7%.

iii) Potato root invasion

Analysis of root samples, taken at 58 DAP, showed that the application of oxamyl had very significantly (P<0.001) reduced the number of juveniles found in the plant roots from a mean of 2530 juveniles/g root in non-oxamyl treated plots down to 140 juveniles/g root in the oxamyl treated plots (Table 4.14). The effect of the oxamyl application could therefore be said to have created a relatively PCN-free control treatment against which the other PCN infected plants and treatments could be compared.

iv) Pf/Pi ratios

The Pf/Pi ratios were not significantly affected by any of the treatments (Table 4.14). The mean Pf/Pi ratio of 0.09 shows that the initial population was severely reduced within this experiment.

Table 4.14. Initial (Pi) and final (Pf) PCN population densities (eggs/g soil), Pf/Pi ratios and potato root invasion by PCN (juveniles/g root) at 58 DAP in an investigation of the growth and yield response to supplementary foliar N and oxamyl of potatoes infected by potato cyst nematodes.

treatment	Pi (eggs/g soil)	Pf (eggs/g soil)	Pf/Pi	root invasion (juveniles/g root)
Std + O [b]	67	4	0.06	140
Std	82	9	0.12	2560
Std + Fol 2% N	84	6	0.08	2810
Std + Fol 4% N	62	9	0.11	2660
Std + Fol 6% N	85	7	0.08	2090
mean	76	7	0.09	2052
significance (P =)	n.s.	n.s.	n.s.	<0.001
SED	15.2	4.0	0.054	323.0
d.f.	16	16	16	16
CV%	32.3	92.7	93.9	24.9

[a] see table 4.2.

4.4.2 Plant growth

i) Plant emergence

The rate of plant emergence was measured on six dates from 33 to 49 DAP. At 33, 35 and 37 DAP the percentage of plants emerged was significantly higher in plots which had been treated with oxamyl (P = 0.03, 0.004 and 0.03 respectively) (Table 4.15). None of the nutrient treatments had been applied by the end of the emergence assessments and, therefore, the significant differences between the standard treatment without oxamyl and the 6% foliar N treatment at 33 DAP, and the 2% foliar N treatment and all other treatments at 42 DAP, cannot be attributed to foliar treatments (Table 4.15). Two methods of statistical analysis were used for further investigation of this anomaly: linear regression, to identify possible relationships between the rate of plant emergence and Pi, $\log_e$ Pi, root invasion or $\log_e$ root invasion, and covariance analysis to remove any underlying differences in PCN population densities between plots. At 33 and 42 DAP the linear regressions (results not shown) showed no relationship between Pi, $\log_e$ Pi or root invasion and the rate of plant emergence. The $\log_e$ root invasion showed some evidence (P = 0.043) of a relationship at 33 DAP but only gave an adjusted r^2 of 0.13, suggesting that very little of the variability in percentage emergence had been accounted for by the root invasion. The requirement for a linear relationship between the two variates to satisfy the conditions of covariance use (Pearce, Clarke & Dyke, 1988) appeared only to have been achieved by the $\log_e$ of root invasion at 33 DAP. When the $\log_e$ root invasion analysis of covariance was carried out, all significant differences were removed but very little difference was made to the actual values (results not shown). The conclusion must be that the difference in the rate of plant emergence between treatments cannot be attributed to differences in PCN pressure measured by Pi or root invasion at 58 DAP. However, if there had been a greater range in Pi across the experiment the conclusion might have been different.

Table 4.15. The percentage emergence of potato plants in an investigation of the growth and yield response to supplementary foliar N and oxamyl of potatoes infected by potato cyst nematodes.

	days after planting					
treatment	33	35	37	40	42	49
Std + O [b]	27.3	50.0	72.7	83.6	93.4	100
Std	14.7	32.4	52.8	78.8	95.8	100
Std + Fol 2% N	20.1	36.7	56.0	79.6	85.9	100
Std + Fol 4% N	16.3	33.0	58.9	79.3	91.0	100
Std + Fol 6% N	23.1	40.2	61.0	80.5	91.5	100
mean	20.3	38.4	60.3	80.4	91.5	100
significance (P =)	0.03	0.004	0.03	n.s.	0.007	n.a.[b]
SED	3.85	4.22	5.73	3.54	2.27	n.a
d.f.	16	16	16	16	16	n.a.
CV%	30.0	17.4	15.0	7.0	3.9	n.a.

[a] see table 4.2.

[b] analysis not applicable as all plots had attained 100% emergence.

ii) Percentage ground cover

The percentage ground cover, estimated on 10 dates throughout the growing period, were significantly (P<0.001) higher at 49, 56, 68, 76, 85, 93, 104 and 120 DAP and significantly (P = 0.019) lower at 146 DAP in plots which had been treated with oxamyl. The statistical analysis of percentage ground cover was by standard Anova for the first three dates of assessment (49, 56 and 68 DAP) after which foliar N applications commenced and, thereafter, statistical analysis of responses to increasing rates of foliar N was made. At 49 DAP the standard treatment, without oxamyl, had significantly less ground cover than did the plots allocated for the 6% foliar N application. There were no significant differences at 56 or 68

DAP. There were no significant responses to N rate on any date but there was evidence ($P = 0.051$) of a linear response at 76 DAP. In the plots not treated with oxamyl, the 4 and 6% foliar N applications gave the highest (non significant) mean percentage ground cover for the whole growing period (Table 4.16a & 4.16b).

iii) Plant fresh and dry weight

Whole plants were removed from plots at 58 DAP, before the application of foliar nutrients. Both fresh and dryweights were significantly ($P<0.001$) heavier where plants came from plots treated with oxamyl. There were no significant differences between the weights of plants from plots not treated with oxamyl, suggesting that, as no foliar applications had been applied at this time, these plants were comparable (Table 4.17).

iv) Chlorophyll content

The chlorophyll content of the fourth leaf from the top of the plant was measured at 6 dates during the growth of the crop. The first measurements, taken two days before the commencement of foliar N applications at 66 DAP, indicated that plants in plots treated with oxamyl had significantly ($P = 0.028$) lower chlorophyll content than those in plots allocated for the 2% and 4% foliar N treatments. There were no significant differences or rate responses at 84 or 98 DAP. The chlorophyll content at 112, 119 and 133 DAP was significantly ($P<0.001$) lower in plants from oxamyl treated plots than in plants from plots not treated with oxamyl. In plots not treated with oxamyl, the application of the 6% foliar N significantly increased chlorophyll content above that measured for the standard and 2% foliar N treatment, at 98 DAP, and above that for the standard treatment at 119 DAP. Significant linear increases to increasing rates of foliar N were seen at 112 DAP ($P = 0.019$) and 119 DAP ($P = 0.003$) (Table 4.18).

Table 4.16a. The percentage ground cover of potato plants in an investigation of the growth and yield response to supplementary foliar N and oxamyl of potatoes infected by potato cyst nematodes.

treatment	days after planting				
	49	56	68	76 [a]	85
Std + O [b]	32.4	48.4	85.2	97.0	97.2
Std	16.6	28.4	52.2	56.8	58.8
Std + Fol 2% N	18.0	27.8	53.6	57.8	59.4
Std + Fol 4% N	19.4	27.8	54.0	62.8	64.4
Std + Fol 6% N	19.8	29.4	54.8	61.0	62.6
mean	21.2	32.4	60.0	67.1	68.5
Overall SED	1.51	1.70	2.65	2.63	3.95
d.f.	16	16	16	16	16
CV%	11.2	8.3	7.0	6.2	9.1
<u>significance (P =)</u>					
overall	<0.001	<0.001	<0.001	<0.001	<0.001
linear	n.a.[c]	n.a.	n.a.	(0.051)	n.s.
quadratic	n.a.	n.a.	n.a.	n.s.	n.s.
cubic	n.a.	n.a.	n.a.	n.s.	n.s.

[a] 12 days after first foliar nutrient applications

[b] see table 4.2.

[c] analysis not applicable as no foliar treatments had been applied.

Table 4.16b. The percentage ground cover of potato plants in an investigation of the growth and yield response to supplementary foliar N and oxamyl of potatoes infected by potato cyst nematodes.

treatment	days after planting 93	104	120	133	146	season mean
Std + O [a]	98.0	97.4	89.4	30.4	5.0	68.0
Std	56.6	57.2	58.2	38.4	11.2	43.4
Std + Fol 2% N	57.0	61.0	57.0	32.8	8.8	43.3
Std + Fol 4% N	62.4	63.4	59.4	33.2	12.8	46.0
Std + Fol 6% N	61.6	61.2	63.6	37.6	12.2	46.4
mean	67.1	68.0	65.5	34.5	10.0	49.3
overall SED	4.31	4.83	4.47	7.81	2.25	2.46
d.f.	16	16	16	16	16	16
CV%	10.2	11.2	10.8	35.8	35.5	7.9
<u>significance (*P* =)</u>						
overall	<0.001	<0.001	<0.001	n.s.	0.019	<0.001
linear	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
quadratic	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
cubic	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

[a] see table 4.2.

Table 4.17. Fresh and dry weight of potato plants, 58 DAP, in an investigation of the growth and yield response to supplementary foliar N and oxamyl of potatoes infected by potato cyst nematodes.

	fresh weight (g)		dry weight (g)	
treatment	Log_e	back-trans [a]	Log_e	back-trans
Std + O [b]	5.926	375	3.360	28.8
Std	4.799	121	2.333	10.3
Std + Fol 2% N	4.681	108	2.226	9.3
Std + Fol 4% N	4.815	123	2.348	10.5
Std + Fol 6% N	4.736	114	2.274	9.7
mean	4.992		2.508	
significance (P=)	<0.001		<0.001	
overall SED	0.1580		0.1601	
d.f.	16		16	
CV%	5.0		10.1	

[a] back-trans = Log_e mean values back-transformed to indicate real values

[b] see table 4.2.

increasing rates of foliar N in the 40-60mm grade. Throughout the range of grades (except the >80mm) the application of increasing rates of foliar N gave small, non- significant, increases in yield (Table 4.19).

Table 4.19. Potato tuber yield (t/ha) at harvest (147 DAP) and tolerance ratio of yield in an investigation of the growth and yield response to supplementary foliar N and oxamyl of potatoes infected by potato cyst nematodes.

	size grade (mm)						
treatment	<40	40-60	60-80	>80	ware	total	tolerance ratio %
Std + O [a]	2.02	32.4	16.3	0.29	48.9	52.0	100
Std	1.53	12.3	10.9	0.00	23.2	24.7	47.6
Std + Fol 2% N	1.52	13.5	8.6	0.22	22.4	23.9	46.0
Std + Fol 4% N	1.63	14.7	11.5	0.79	27.0	28.6	55.0
Std + Fol 6% N	1.76	15.3	12.0	0.58	27.8	29.5	56.9
mean	1.89	17.6	11.8	0.37	29.8	31.7	61.1
overall SED	0.195	1.45	2.34	n.a.	3.21	3.23	6.21
d.f.	16	16	16	n.a.	16	16	16
CV%	16.3	13.0	31.2	n.a.	17.0	16.1	16.1
<u>significance (*P* =)</u>							
overall	<0.001	<0.001	n.s.	n.a.	<0.001	<0.001	<0.001
linear	n.s.	0.045	n.s.	n.a.	n.s.	n.s.	n.s.
quadratic	n.a.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
cubic	n.a.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

[a] see table 4.2.

i) Tolerance to PCN

The tolerance of potato plants to PCN infection, expressed as a percentage of the yield produced by plants in plots treated with oxamyl, suggested that the 4% and 6% foliar N applications had increased the tolerance by 7.4% and 9.3% respectively. These were not significant improvements however (Table 4.19).

Table 4.20. Effect of covariance on the analysis of potato total tuber yields (t/ha) in an investigation of the growth and yield response to supplementary foliar N and oxamyl of potatoes infected by potato cyst nematodes.

	covariate			
treatment	none	Pi [a]	invasion [b]	$\log_e$ invasion [c]
Std + O [d]	52.0	51.1	48.7	53.2
Std	24.7	25.3	25.6	24.4
Std + Fol 2% N	23.9	24.7	25.2	23.5
Std + Fol 4% N	28.6	27.2	29.6	28.3
Std + Fol 6% N	29.5	30.4	29.3	29.6
mean	31.7	31.7	31.7	31.7
significance (P =)	<0.001	<0.001	0.043	n.s.
covariance (P =)	n.a.	n.s.	n.s.	n.s.
overall SED	3.23	3.06	5.15	10.80
d.f.	16	16	16	16
CV%	16.1	14.8	16.4	16.6

[a] Initial PCN population

[b] PCN invasion of roots (juveniles/g root) 58 days after planting.

[c] $\log_e$ transformed values of PCN invasion of roots (juveniles/g root) 61 days after planting

[d] see table 4.2.

ii) Effect of covariance on yield

The total tuber yield was analysed by covariance analysis to remove underlying differences between plots of initial PCN population (Pi), potato root invasion by PCN at 58 DAP and the $\log_e$ transformation of potato root invasion by PCN at 58 DAP. The yield in oxamyl treated plots remained significantly higher than yields in plots not treated with oxamyl where the Pi (P<0.001) and invasion (P = 0.043) covariates were used. Where the $\log_e$ of root invasion was used the yield of oxamyl treated plots remained substantially higher than plots not treated with oxamyl but the difference was not significant (Table 4.20).

iii) PCN relationship to total crop yield

a) Simple linear relationship

There was a significant (P = 0.048) relationship between Pi and total crop yield but with an r^2 of only 0.12 the variance between the two variables was not well explained. There were significant (P<0.001) linear relationships of both root invasion and the $\log_e$ root invasion on total yield (Figure 4.9 and 4.10). The $\log_e$ root invasion variate related better to total yield (r^2 = 0.79) than did the untransformed root invasion (r^2 = 0.75).

b) Blocked experiment relationship

Although simple linear regressions are commonly used to describe relationships within 'blocked' experimental designs, their use is not strictly correct in this context. Therefore, the effects of Pi, root invasion and $\log_e$ root invasion on the total yield were further analysed by regression of blocked experiment data. No significant relationship was found between the Pi and the total crop yield when the effects of treatments were accounted for. However, significant (P<0.001) relationships between root invasion and $\log_e$ root invasion on the total yield were found again, with untransformed root invasion attaining an r^2 value of 0.82 (Figure 4.11) and $\log_e$ root invasion a value of 0.81. Thus root invasion or $\log_e$ root invasion are the most suitable covariates.

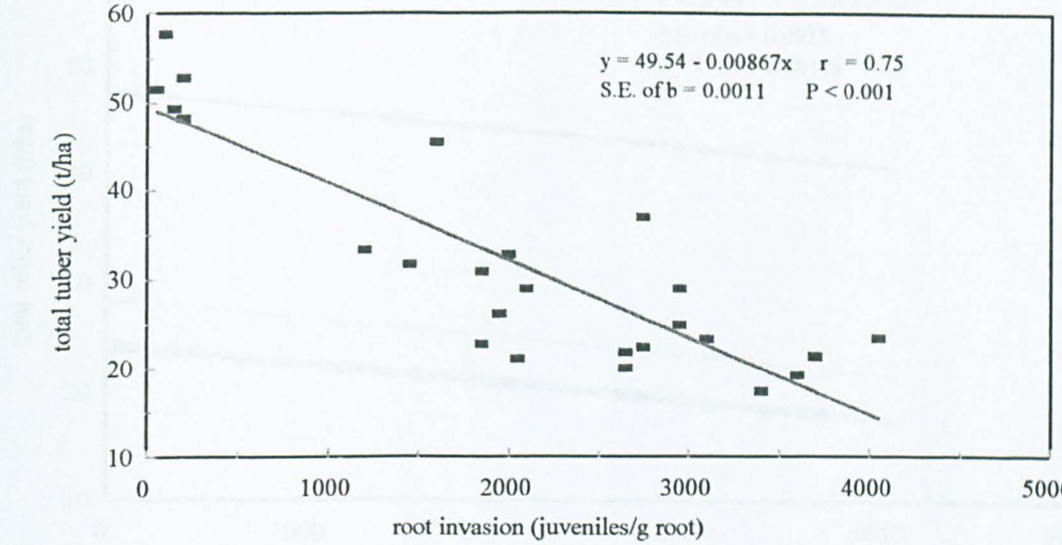

Figure 4.9. The simple linear relationship between PCN root invasion at 58 DAP and total tuber yield at harvest (147 DAP) in an investigation of the growth and yield response to supplementary foliar N and oxamyl of potatoes infected by potato cyst nematodes.

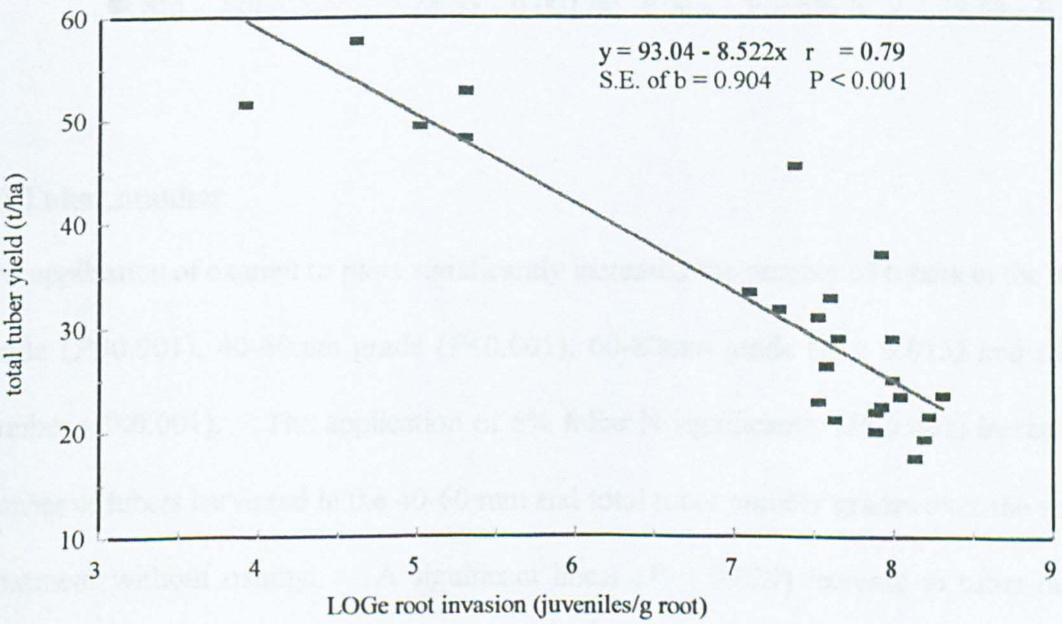

Figure 4.10. The simple linear relationship between $\log_e$ root invasion at 58 DAP and total tuber yield at harvest (147 DAP) in an investigation of the growth and yield response to supplementary foliar N and oxamyl of potatoes infected by potato cyst nematode.

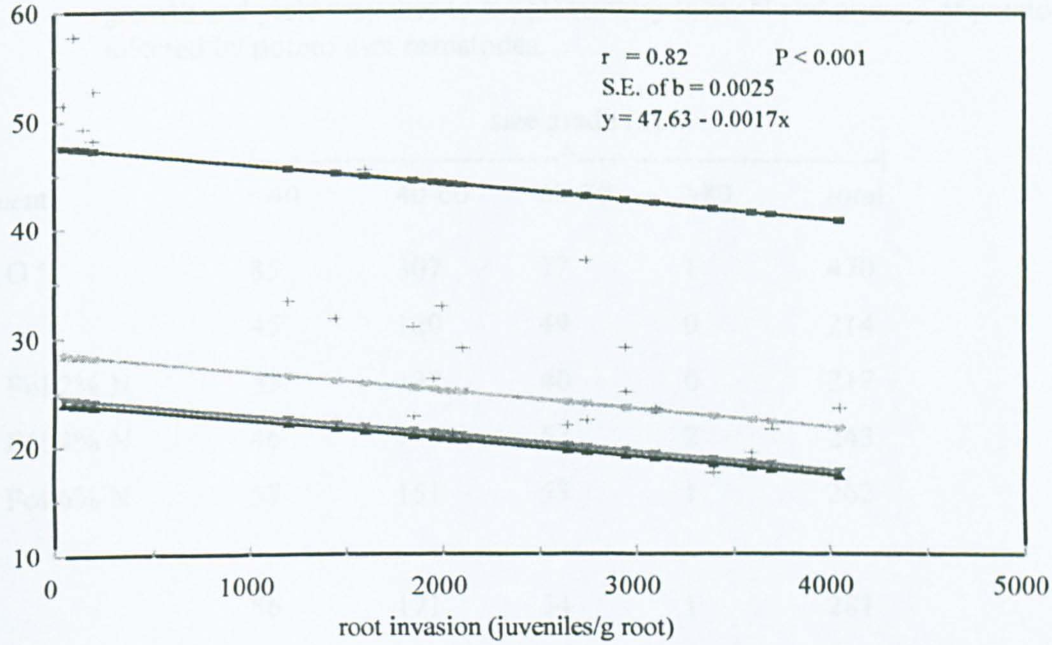

Figure 4.11. Linear relationship (blocked experiment) between potato root invasion (juveniles/g root) at 58 DAP and total tuber yield at harvest (147 DAP) in an investigation of the growth and yield response to foliar N and oxamyl of potatoes infected by potato cyst nematode.

[a] regression line parameters : ■ Std + O y = 47.63 - 0.0017x;
▼ Std y = 24.54 - 0.0017x; ▲ Std + Fol 2% N y = 24.10 - 0.0017x
● Std + Fol 4% N y = 28.55 - 0.0017x; ⊠ Std + Fol 6% N y = 28.54 - 0.0017x

iv) Tuber number

The application of oxamyl to plots significantly increased the number of tubers in the <40mm grade (P<0.001), 40-60mm grade (P<0.001), 60-80mm grade (P = 0.015) and the total number (P<0.001). The application of 6% foliar N significantly (P<0.001) increased the number of tubers harvested in the 40-60 mm and total tuber number grades over the standard treatment without oxamyl. A significant linear (P = 0.029) increase in tuber numbers occurred from increasing rates of foliar N application (Table 4.21).

Table 4.21. Potato tuber number per plot at harvest (147 DAP) in an investigation of the growth and yield response to supplementary foliar N and oxamyl of potatoes infected by potato cyst nematodes.

	size grade (mm)				
treatment	<40	40-60	60-80	>80	total
Std + O [a]	85	307	77	1	470
Std	45	120	49	0	214
Std + Fol 2% N	45	132	40	0	217
Std + Fol 4% N	46	143	52	2	243
Std + Fol 6% N	57	151	53	1	262
mean	56	171	54	1	281
overall SED	8.3	13.7	9.5	n.a.[b]	19.6
d.f.	16	16	16	n.a.	16
CV%	23.6	12.7	27.8	n.a.	11.0
<u>significance (*P* =)</u>					
overall	<0.001	<0.001	0.015	n.a.	<0.001
linear	n.s.	0.029	n.s.	n.a.	0.015
quadratic	n.s.	n.s.	n.s.	n.s.	n.s.
cubic	n.s.	n.s.	n.s.	n.s.	n.s.

[a] see table 4.2.

v) Tuber dry matter

The application of oxamyl to plots produced a significantly ($P = 0.024$) higher percentage dry matter in tubers than in plots not treated with oxamyl. There were no significant effects of foliar N on the percentage dry matter (Table 4.22).

Table 4.22. Percentage tuber dry matter at harvest (147 DAP) in an investigation of the growth and yield response to supplementary foliar N and oxamyl of potatoes infected by potato cyst nematodes.

treatment	dry matter %
Std + O [a]	22.45
Std	21.05
Std + Fol 2% N	20.50
Std + Fol 4% N	21.35
Std + Fol 6% N	21.15
mean	21.30
significance (*P*=)	0.024
overall SED	0.523
d.f.	16
CV%	3.9

[a] see table 4.2.

4.4.4 Nutrient status

i) Whole plant at 58 DAP

The application of oxamyl to plots produced significantly higher concentrations of N (P = 0.003), P and K (P<0.001) in the dry matter than that measured in any plants from plots not treated with oxamyl. No foliar N applications had been made by this time (58 DAP) but a significantly (P = 0.003) higher N concentration was measured between plants from plots allocated for the 6% foliar N treatment than in those from plots allocated for the standard treatment without oxamyl or foliar N applications (Table 4.23).

ii) Fourth leaf at 98 DAP

Plants from plots treated with oxamyl were shown to have significantly (P<0.001) lower concentrations of N in the fourth leaf (plus petiole) than plant's from plots not treated with oxamyl. Plants from the standard non oxamyl plots contained a significantly ($P<0.001$) lower N concentration than all plants which had received foliar N applications. Applying foliar N at the 6% rate produced a significantly ($P<0.001$) higher N concentration than either the 2% or 4% foliar N applications (Table 4.23). The increases in N concentration showed significant linear ($P<0.001$) and also significant cubic ($P = 0.014$) correlations with the increasing rates of foliar N application.

Table 4.23. Nutrient concentrations of whole potato plant dry matter, at 58 DAP, and potato fourth leaf plus petiole at 98 DAP, in an investigation of the growth and yield response to supplementary foliar N and oxamyl of potatoes infected by potato cyst nematodes.

	58 DAP			98 DAP
treatment	%N	%P	%K	%N
Std + O [a]	3.84	0.376	6.27	3.31
Std	3.40	0.273	4.86	3.54
Std + Fol 2% N	3.58	0.276	4.78	4.03
Std + Fol 4% N	3.50	0.282	4.81	4.00
Std + Fol 6% N	3.65	0.295	5.08	4.47
mean	3.59	0.300	5.16	3.87
overall SED	0.092	0.0145	0.146	0.113
d.f.	16	16	16	16
CV%	4.0	7.6	4.5	4.6
<u>significance (P =)</u>				
overall	0.003	<0.001	<0.001	<0.001
linear	n.a.[b]	n.a.	n.a.	<0.001
quadratic	n.a.	n.a.	n.a.	n.s.
cubic	n.a.	n.a.	n.a.	0.014

[a] see table 4.2.

[b] n.a. analysis not applicable as foliar nitrogen had not been applied at this time.

iii) PCN effect on nutrient status

a) Simple linear relationship

The initial PCN population, Pi, was not related to the N, P or K concentration in the whole plant dry matter at 58 DAP. The r^2 values derived for the relationships were only 0.08 for N, 0.10 for P and 0.01 for K. The numbers of PCN juveniles counted in the plant roots at 58 DAP bore some relation to the nutrient status of the plant; root invasion was significantly ($P<0.001$) related to N, P and K concentration with the concentration of all three nutrients decreasing with increasing numbers of PCN juveniles in the potato roots. The r^2 values were 0.36 for N, 0.67 for P and 0.79 for K, suggesting that N, P and K concentration of potato plants can be linked to root invasion by PCN and that the strongest link arises with the K concentration (Figure 4.12 and 4.13).

b) Blocked experiment relationship

There were no significant relationships between Pi and N, P or K concentrations.

Analysis of the experiment data with blocked experiment regression showed pronounced PCN root invasion effects on the N, P and K concentrations of whole plant dry matter at 58 DAP. Root invasion significantly ($P = 0.012$) reduced the N concentration and an adjusted r^2 of 0.51 shows that much more of the variance was explained with this analysis than with the simple regression. Root invasion significantly ($P<0.001$) reduced the P concentration and an adjusted r^2 of 0.78 indicates quite a strong relationship. Root invasion also significantly ($P<0.001$) reduced the K concentration and an adjusted r^2 of 0.87 suggests a very strong association between these two variables at 58 DAP.

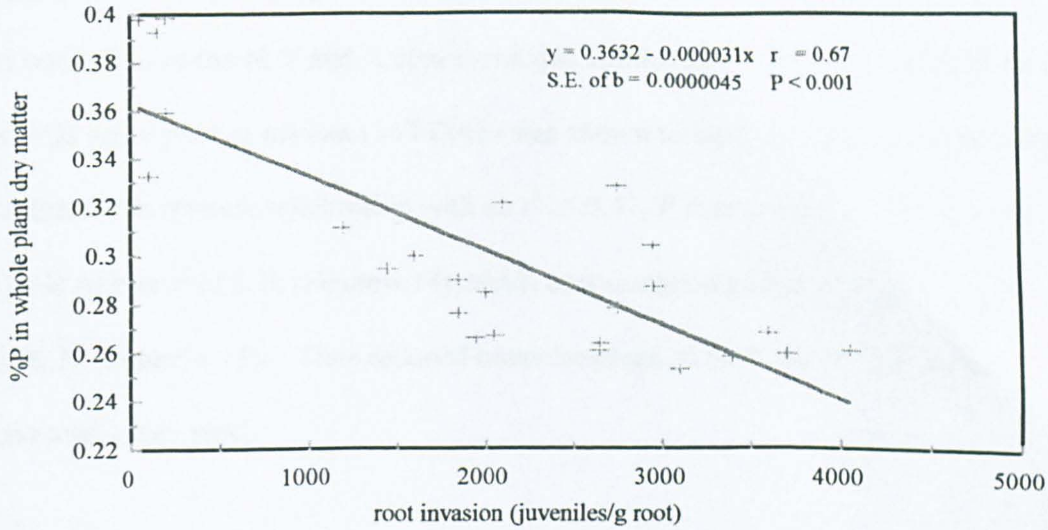

Figure 4.12. The simple linear relationship of PCN root invasion, at 58 DAP, with the %P measured in whole plant dry matter in an investigation of the growth and yield response to supplementary foliar N and oxamyl of potatoes infected by potato cyst nematodes.

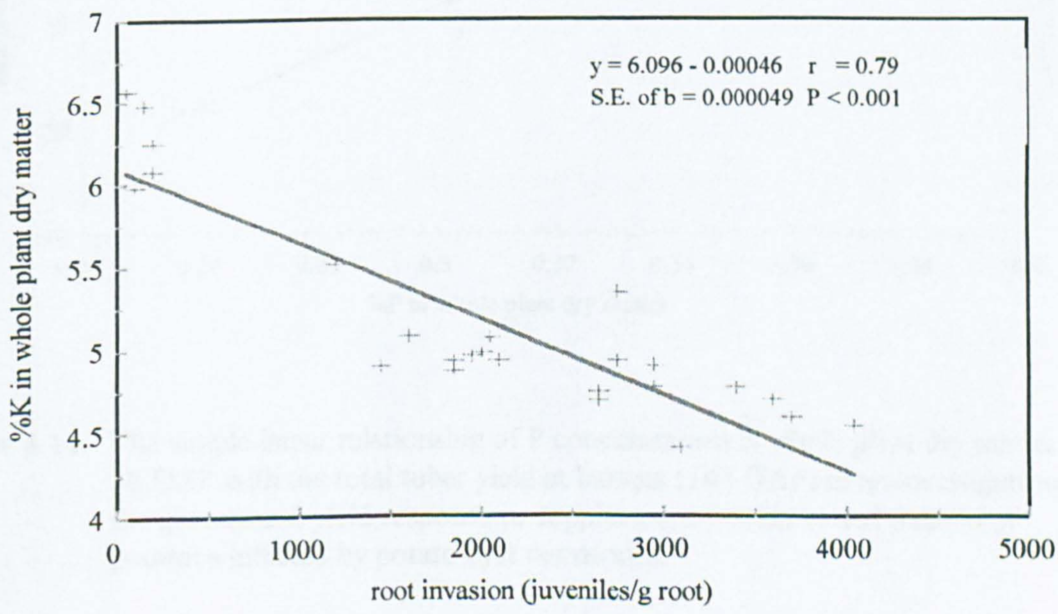

Figure 4.13. The simple linear relationship of PCN root invasion, at 58 DAP, with the %K measured in whole plant dry matter in an investigation of the growth and yield response to supplementary foliar N and oxamyl of potatoes infected by potato cyst nematodes.

iv) Nutrient relationship to tuber yield

a) Simple linear relationship

The relationships of the N, P and K concentrations within whole plant dry matter at 48 DAP to the total tuber yield at harvest (147 DAP) was shown to be quite strong: N concentration demonstrated the poorest relationship with an r^2 of 0.47, P concentration was well related to tuber yield with an r^2 of 0.76 (Figure 4.14); and K concentration gave the best association with an r^2 of 0.78 (Figure 4.15). Thus reduced concentrations of N, P and K are associated with reduced total tuber yield.

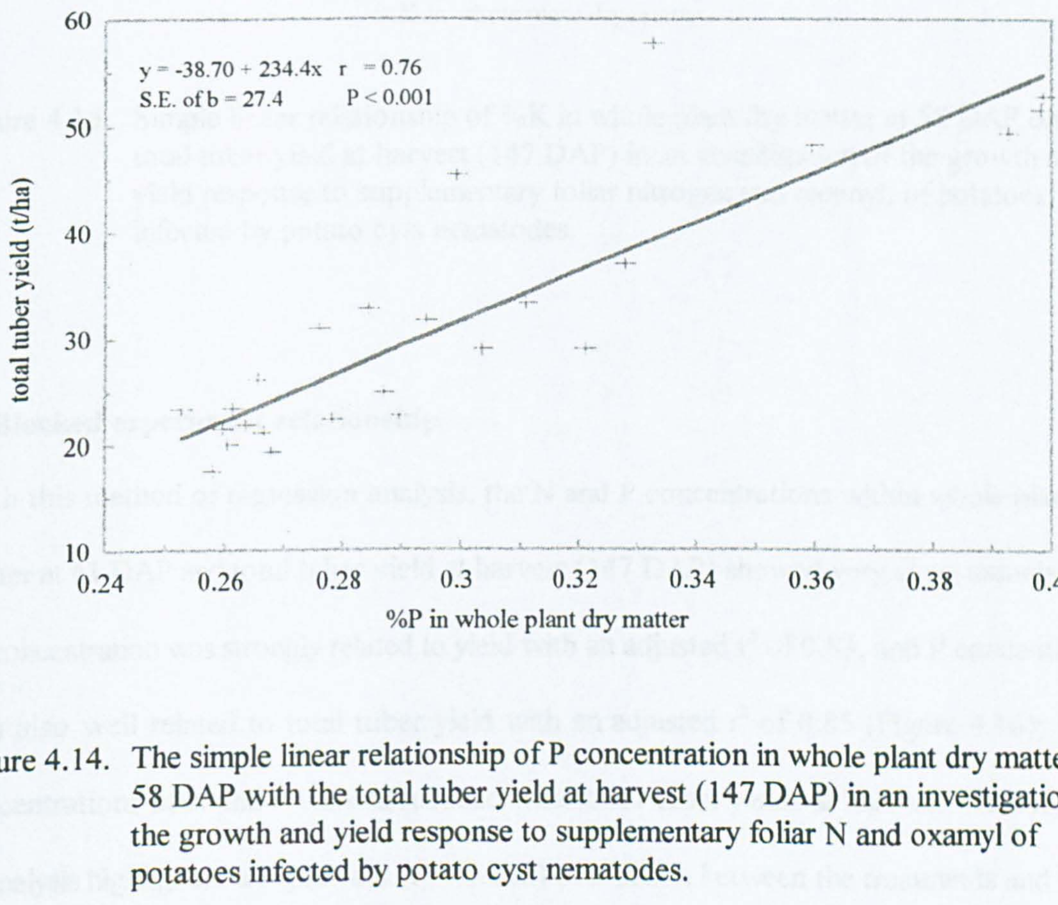

Figure 4.14. The simple linear relationship of P concentration in whole plant dry matter at 58 DAP with the total tuber yield at harvest (147 DAP) in an investigation of the growth and yield response to supplementary foliar N and oxamyl of potatoes infected by potato cyst nematodes.

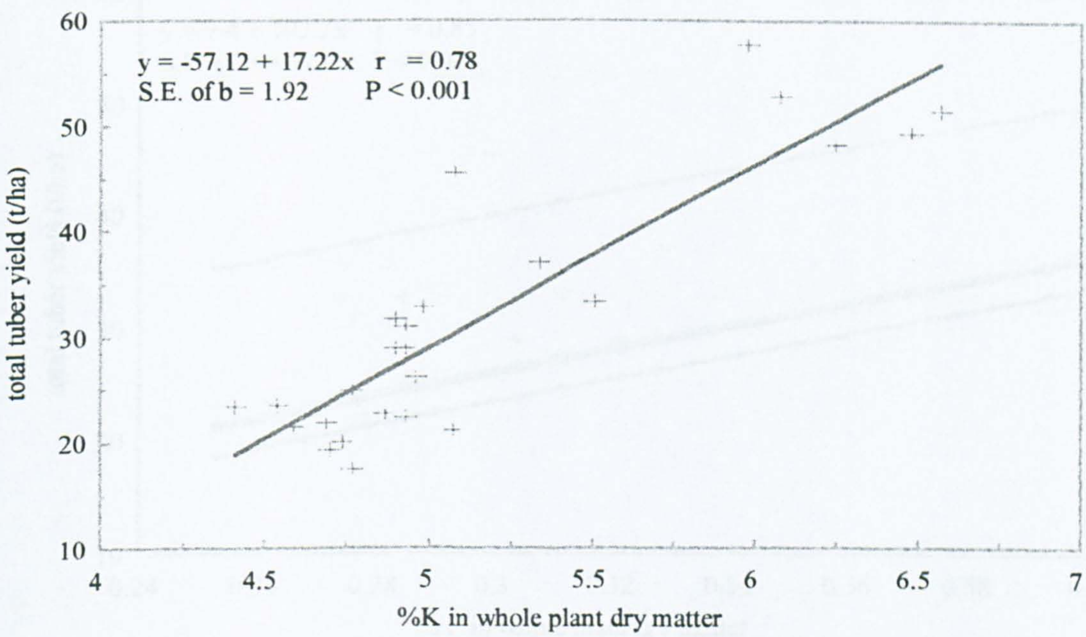

Figure 4.15. Simple linear relationship of %K in whole plant dry matter at 58 DAP on the total tuber yield at harvest (147 DAP) in an investigation of the growth and yield response to supplementary foliar nitrogen and oxamyl, of potatoes infected by potato cyst nematodes.

b) Blocked experiment relationship

With this method of regression analysis, the N and P concentrations within whole plant dry matter at 61 DAP and total tuber yield at harvest (147 DAP) showed very close associations. N concentration was strongly related to yield with an adjusted r^2 of 0.83, and P concentration was also well related to total tuber yield with an adjusted r^2 of 0.85 (Figure 4.16); lower concentrations of N and P were associated with lower tuber yields at harvest. This method of analysis highlighted a significant ($P = 0.002$) interaction between the treatments and the K concentration, which made the method unsuitable for use with this variate.

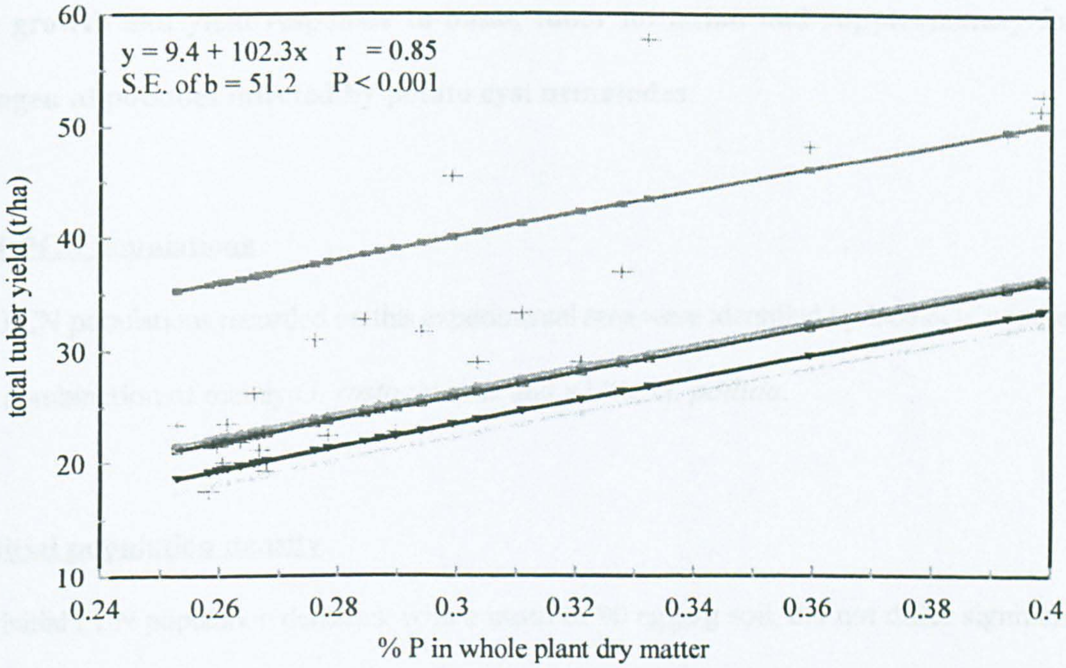

Figure 4.16. Blocked experiment relationship of P concentration in whole plant dry matter at 58 DAP and the total tuber yield at harvest (147 DAP) in an investigation of the growth and yield response to supplementary foliar nitrogen and oxamyl of potatoes infected by potato cyst nematodes.

[a] Regression line parameters :

		■ Std + O	y = 9.4 + 102.3x;
▼ Std	y = -7.22 + 102.3x;	▲ Std + Fol 2% N	y = -8.41 + 102.3x
● Std + Fol 4% N	y = -4.28 + 102.3x;	⊠ Std + Fol 6% N	y = -4.73 + 102.3x

4.5 Results of experiment three

The growth and yield responses to basal, tuber initiation and supplementary foliar nitrogen of potatoes infected by potato cyst nematodes.

4.5.1 PCN populations

The PCN populations recorded on this experimental area were identified by isoelectric focusing as a combination of mainly *G. rostochiensis* and a little G. *pallida*.

i) Initial population density

The initial PCN population densities, with a mean of 90 eggs/g soil, did not differ significantly between treatments. The lowest mean treatment population density of 71 eggs/g soil was substantially lower than the highest mean treatment population density of 116 eggs/g soil, and this was reflected by the CV of 33.5%, which showed the variability on the site (Table 4.24).

ii) Final population density

The final PCN population densities were not significantly affected by any of the treatments (Table 4.24). The population densities were considerably reduced from a mean initial population density of 90 eggs/g soil to only 8 eggs/g soil. The CV of 100.5% for Pf shows there was considerable variation within the experiment.

iii) Potato root invasion

Analysis of root samples, taken at 56 DAP, showed that the application of oxamyl had very significantly ($P<0.001$) reduced the number of juveniles found in the plant roots from a mean of 1569 juveniles/g root down to 160 juveniles/g root (Table 4.24). Oxamyl application could therefore be said to have created a relatively PCN uninfected control treatment against which the other PCN infected plants and treatmemts could be compared.

iv) Pf/Pi ratios

The Pf/Pi ratio was not significantly affected by any of the basal, tuber initiation, foliar N or oxamyl applications (Table 4.24). The mean Pf/Pi ratio of 0.09 shows that PCN multiplication was largely prevented and that the initial population was severely reduced within this experiment.

4.5.2 Plant growth

i) Plant emergence

Plant emergence was measured on seven dates from 28 to 49 DAP. At 33, 35, 37, 40 and 42 DAP the percentage of plants emerged was significantly higher in plots which had been treated with oxamyl (P <0.001, 0.001, 0.001, 0.008 and 0.008 respectively) (Table 4.25). There were no significant differences at 28 or 49 DAP. Although there were no foliar N applications during the assessment period, a significantly (P<0.001) greater number of plants emerged in the Std + F than in the Std (control) treatment at 33 DAP (Table 4.25). Linear regression to identify a possible relationship between plant emergence and Pi, Log_e Pi, root invasion and Log_e root invasion (results not shown) showed no relationship between Pi or log_e Pi, root invasion or log_e root invasion and plant emergence at 33 DAP. At 40 DAP in plots where all of the basal N was applied at planting, significantly (P = 0.048) fewer plants emerged than where the high rate of basal N was applied at planting (Table 4.25). Linear regression of Pi, log_e Pi, root invasion and log_e root invasion on plant emergence showed no significant relationships (results not shown). It cannot be suggested that the differences in plant emergence seen within plots not treated with oxamyl were linked to differences in PCN pressure but the difference at 40 DAP could be the result of applying all of the basal N at planting.

Table 4.24. Initial (Pi) and final (Pf) PCN population densities (eggs/g soil), Pf/Pi ratios and potato root invasion by PCN (juveniles/g root) at 56 DAP in an investigation of the growth and yield response to oxamyl and basal, tuber initiation and supplementary foliar N of potatoes infected by potato cyst nematodes.

treatment	Pi (eggs/g soil)	Pf (eggs/g soil)	Pf/Pi	root invasion (juveniles/g root)
Std + O [a]	84	5	0.07	160
Std	100	8	0.07	1730
Std + F	78	11	0.14	1780
HIGH + F	116	6	0.05	1244
ALL + F	71	8	0.12	1520
mean	90	8	0.09	1287
SED	18.9	4.8	0.058	312.4
d.f.	16	16	16	16
CV%	33.5	100.5	100.4	38.4
<u>significance ($P =$)</u>				
overall	n.s.	n.s.	n.s.	<0.001
Std + O vs non oxamyl trts	n.s.	n.s.	n.s.	<0.001
Std vs mean of + F trts	n.s.	n.s.	n.s.	n.s.
Std + F vs mean High & All	n.s.	n.s.	n.s.	n.s.
High + F vs All + F	0.031	n.s.	n.s.	n.s.

[a] see table 4.3.

Table 4.25. The percentage emergence of potato plants in an investigation of the growth and yield response to oxamyl and basal, tuber initiation and supplementary foliar N of potatoes infected by potato cyst nematodes.

	days after planting						
treatment	28	33	35	37	40	42	49
Std +O [a]	8.8	33.2	53.1	77.0	82.4	95.3	100
Std	5.8	15.4	34.1	58.4	77.5	90.1	100
Std + F	5.6	25.5	40.6	63.2	77.5	87.4	100
HIGH + F	6.3	19.7	33.4	58.6	80.3	86.0	100
ALL + F	8.9	20.1	35.4	58.2	76.3	88.4	100
mean	7.1	22.8	39.3	63.1	78.8	89.4	100
SED	2.24	3.22	4.08	5.14	1.85	3.08	n.a
d.f.	16	16	16	16	16	16	n.a.
CV%	49.9	22.4	16.4	12.9	3.7	5.4	n.a.
Significance (*P*=)							
overall	n.s.	<0.001	<0.001	0.009	0.029	n.s	n.a.[b]
Std + O vs							
vs non oxamyl trts	n.s.	<0.001	<0.001	<0.001	0.008	0.008	
Std vs mean of +F	n.s.	0.029	n.s.	n.s.	n.s.	n.s.	
Std + F vs							
mean High & All	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	
High + F vs All + F	n.s.	n.s.	n.s.	n.s.	0.048	n.s.	

[a] see table 4.3.

[b] analysis not applicable as all plots had attained 100% emergence.

ii) Plant fresh and dry weight

Whole plants were removed from plots at 56 DAP, and before the application of foliar nutrients. Both fresh and dry-weights were significantly (P<0.001) greater where plants came from plots treated with oxamyl. There were no significant differences between the weights of plants from plots not treated with oxamyl, suggesting that, as no foliar applications had been applied at this time, these plants were comparable (Table 4.26).

Table 4.26. Fresh and dry weights of potato plants, 56 DAP, in an investigation of the growth and yield response to oxamyl and basal, tuber initiation and supplementary foliar N of potatoes infected by potato cyst nematodes.

	fresh weight (g)		dry weight (g)	
treatment	$\log_e$	back-trans [a]	$\log_e$	back-trans
Std +O [b]	5.650	284	3.107	22.4
Std	4.772	118	2.321	10.2
Std + F	4.667	106	2.258	9.6
HIGH + F	4.571	116	2.271	9.7
ALL + F	4.829	125	2.343	10.4
mean	4.934	139	2.460	11.7
overall SED	0.1437		0.1556	
d.f.	16		16	
CV%	4.6		10.0	
<u>Significance (*P* =)</u>				
overall	<0.001		<0.001	
Std + O vs non oxamyl trts	<0.001		<0.001	
Std vs mean of +F trts	n.s.		n.s.	
Std + F vs mean High & All	n.s.		n.s.	
High + F vs All + F	n.s.		n.s.	

[a] back-trans = Log_e mean values back-transformed to indicate real values

[b] see table 4.3.

Table 4.27a. The percentage ground cover of potato plants in an investigation of the growth and yield response to oxamyl and basal, tuber initiation and supplementary foliar N of potatoes infected by potato cyst nematodes.

	days after planting				
treatment	49	56	68	76 [a]	85
Std +O [b]	32.4	49.6	86.6	95.4	98.0
Std	17.6	29.8	54.8	64.0	64.4
Std + F	19.4	35.0	57.8	61.6	66.4
HIGH + F	17.8	29.2	53.0	61.8	62.2
ALL + F	18.8	28.8	58.2	63.4	65.0
mean	21.2	34.5	62.1	69.2	71.2
overall SED	1.88	1.57	2.06	2.46	2.54
d.f.	16	16	16	16	16
CV%	14.1	7.2	5.3	5.6	5.6
<u>significance (*P* =)</u>					
overall	<0.001	<0.001	<0.001	<0.001	<0.001
Std + O vs non oxamyl trts	<0.001	<0.001	<0.001	<0.001	<0.001
Std vs mean of + F trts	n.s.	n.s.	n.s.	n.s.	n.s.
Std + F vs mean High & All	n.s.	<0.001	n.s.	n.s.	n.s.
High + F vs All + F	n.s.	n.s.	0.023	n.s.	n.s.

[a] 12 days after first foliar nutrient applications

[b] see table 4.3.

<u>iii) Percentage ground cover</u>

The percentage ground cover estimates made on 10 dates through the growing period, were significantly (*P*<0.001) higher at 49, 56, 68, 76, 85, 93, 104 and 120 DAP in plots which had been treated with oxamyl. At 56 DAP plots allocated for the Std + Foliar N treatment had significantly (*P*<0.001) higher ground cover than all other plots not treated with oxamyl including the essentially similar Std treatment, although no foliar N had been applied. By 68

DAP this anomaly had disappeared and only the plots given all of the basal N at planting showed significant (P = 0.023) differences. The application of foliar nutrients, which began at 68 DAP, had no significant effect at 76, 85, and 93 DAP. At 104, 120 and 146 DAP, the percentage ground cover was significantly (P<0.001) lower in plots which had received all of the basal N at planting (Table 4.27a & 27b).

Table 4.27b. The percentage ground cover of potato plants in an investigation of the growth and yield response to oxamyl and basal, tuber initiation and supplementary foliar N of potatoes infected by potato cyst nematodes.

treatment	days after planting 93	104	120	133	146	season mean
Std +O [a]	98.8	96.6	90.6	25.4	3.8	67.7
Std	64.4	62.4	51.8	24.4	5.2	43.9
Std + F	65.8	63.0	53.4	26.2	6.2	45.5
HIGH + F	61.4	59.4	48.4	20.0	6.8	42.0
ALL + F	62.8	53.0	32.0	8.2	1.4	39.2
mean	70.6	66.9	55.2	20.8	4.7	47.7
overall SED	2.72	3.98	4.04	6.67	2.22	1.43
d.f.	16	16	16	16	16	16
CV%	6.1	9.4	11.6	50.6	75.0	4.7
<u>significance (P =)</u>						
overall	<0.001	<0.001	<0.001	n.s.	n.s.	<0.001
Std +O vs non oxamyl trts	<0.001	<0.001	<0.001	n.s.	n.s.	<0.001
Std vs mean of + F trts	n.s.	n.s.	0.044	n.s.	n.s.	n.s.
Std +F vs mean High & All	n.s.	n.s.	0.002	n.s.	n.s.	0.001
High + F vs All + F	n.s.	n.s.	<0.001	n.s.	0.027	n.s.

[a] see table 4.3.

4.5.3 Tuber yield

The application of oxamyl to plots significantly ($P<0.001$) improved the tuber yield in all grades. In plots not treated with oxamyl, those receiving all of the basal N at planting produced a significantly ($P = 0.002$) higher yield of <40mm tubers than the plots where N applications were split 50/50 between planting and tuber initiation (Std). There were no significant fertiliser effects in the 40-60mm grade. In the 60-80mm tuber grade, tuber yields were significantly ($P = 0.009$) higher where N applications were split 50/50 between planting and tuber initiation, than where all of the N was applied at planting (ALL + F). This trend continued in the ware and total tuber grades, where the plots in which N applications were split 50/50 between planting and tuber initiation produced significantly ($P = 0.010$) greater yields than plots which had received higher quantities of seedbed N (HIGH + F and ALL + F) (Table 4.28).

i) Tolerance to PCN

The tolerance of potato plants to PCN infection, expressed as a percentage of the yield produced by plants in plots treated with oxamyl, was not significantly affected by altering the ratio of basal N between planting and tuber initiation applications. In treatments where supplementary foliar N was applied the tolerance ratio was significantly ($P = 0.010$) higher where the basal N had been split 50/50 between planting and tuber initiation application (Std + F) (Table 4.28).

Table 4.28. Potato tuber yield (t/ha) at harvest (147days after planting) and tolerance ratio of yield in an investigation of the growth and yield response to oxamyl and basal, tuber initiation and supplementary foliar N of potatoes infected by potato cyst nematodes.

treatment	size grade (mm) <40	40-60	60-80	>80	ware	total	tolerance ratio % [a]
Std + O [b]	2.66	30.1	18.6	0.18	48.9	51.6	100
Std	1.46	14.5	9.7	0.11	24.3	25.7	49.9
Std + F	1.70	15.3	10.9	1.26	27.4	29.1	56.5
HIGH + F	1.72	14.5	8.3	0.00	22.8	24.5	47.6
ALL + F	1.99	14.2	6.7	0.00	20.9	22.9	44.5
mean	1.90	17.7	10.8	n.a.	28.9	30.8	59.7
overall SED	0.249	1.82	1.99	n.a.	2.16	2.15	4.18
d.f.	16	16	16	n.a.	16	16	16
CV%	20.7	16.3	29.1	n.a.	11.8	11.1	11.1
<u>significance (P =)</u>							
overall	0.002	<0.001	<0.001	n.a.	<0.001	<0.001	0.001
Std + O vs							
vs non oxamyl trts	<0.001	<0.001	<0.001	n.a.	<0.001	<0.001	0.001
Std vs mean of + F	n.s.	n.s.	n.s.	n.a.	n.s.	n.s.	n.s.
Std + F vs							
mean High & All	n.s.	n.s.	n.s.	n.a.	0.009	0.010	0.010
High + F vs All + F	n.s.	n.s.	n.s.	n.a.	n.s.	n.s.	n.s.

[a] tolerance ratio calculated as percentage yield of oxamyl treated yield.

[b] see table 4.3.

Table 4.29. Effect of covariance on the analysis of potato total tuber yields (t/ha) in an investigation of the growth and yield response to oxamyl and basal, tuber initiation and supplementary foliar N of potatoes infected by potato cyst nematodes.

treatment	covariance type			
	none	Pi [a]	invasion [b]	$\log_e$ invasion [c]
Std + O [b]	51.6	51.4	55.1	55.5
Std	25.7	26.0	24.3	25.0
Std + F	29.1	28.9	27.6	28.3
HIGH + F	24.5	25.2	24.7	24.4
ALL + F	22.9	22.5	22.2	22.4
mean	30.8	30.8	30.8	30.8
overall SED	2.15	2.29	2.47	2.69
d.f.	16	16	16	16
CV%	11.1	11.2	10.2	9.8
<u>Significance (*P* =)</u>				
overall	<0.001	<0.001	<0.001	<0.001
covariance	n.a.[e]	n.s.	n.s.	n.s.
Std + O vs non oxamyl trts	<0.001	<0.001	<0.001	<0.001
Std vs mean of + F trts	n.s.	n.s.	n.s.	n.s.
Std + F vs mean High & All	0.010	0.015	0.031	0.012
High + F vs All + F	n.s.	n.s.	n.s.	n.s.

[a] Initial PCN population
[b] PCN invasion of roots (juveniles/g root) 61 days after planting.
[c] $\log_e$ transformed values of PCN invasion of roots (juveniles/g root) 61 days after planting
[d] see table 4.3.
[e] not applicable to analysis.

ii) Effect of covariance on yield

The total tuber yield was subjected to covariance analysis to remove underlying plot differences in initial PCN population (Pi), potato root invasion by PCN at 56 DAP and the $\log_e$

transformation of potato root invasion by PCN at 56 DAP. The yield in oxamyl treated plots remained significantly ($P<0.001$) higher than yields in plots not treated with oxamyl irrespective of covariate type (Table 4.29). In plots not treated with oxamyl, the significant total yield improvement in plots where N applications were split 50/50 between planting and tuber initiation, (Std + F), over plots which had received higher quantities of N at planting (HIGH + F and ALL + F) were not affected by covariate analysis (Table 4.29). Neither higher quantities of N at planting nor foliar N applications gave significant yield improvements over the normal basal N treatment.

iii) PCN relationship to total crop yield

Identification of covariates which satisfied the rules of covariance choice:

a) Simple linear relationship

No significant relationship found between Pi or $\log_e$ Pi and total crop yield and no r^2 values could be derived from the data. There were significant linear relationships of both root invasion ($P = 0.005$) and the $\log_e$ root invasion ($P<0.001$) on total yield (Figure 4.17 and 4.18). The $\log_e$ root invasion variate related better to total yield ($r^2 = 0.46$) than did the untransformed root invasion ($r^2 = 0.29$).

b) Blocked experiment relationship

As only the root invasion and $\log_e$ root invasion showed any relationship to total yield these covariates were further analysed by regression of blocked experiment data. Significant ($P<0.001$) relationships were found with both covariates. The variance of yield and covariates were well explained for both, with r^2 values of 0.93 for the root invasion and 0.92 for the $\log_e$ root invasion. Unlike the previous experiments, however, the relationship was positive, with increasing yields as invasion increased (Figure 4.19).

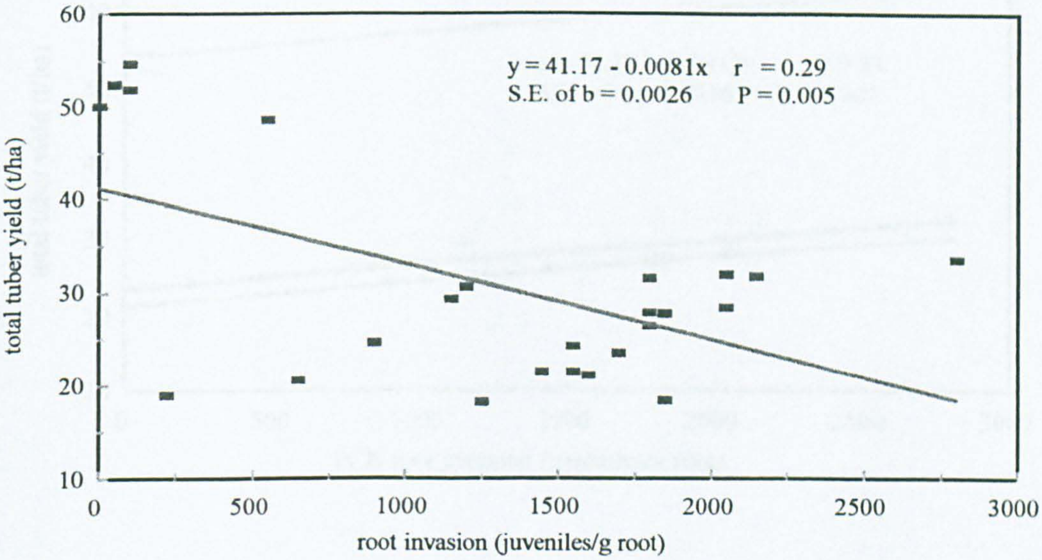

Figure 4.17. The simple linear relationship of PCN root invasion at 56 DAP on the total tuber yield at harvest (147 DAP) in an investigation of the growth and yield response to oxamyl and basal, tuber initiation and foliar N of potatoes infected by potato cyst nematodes.

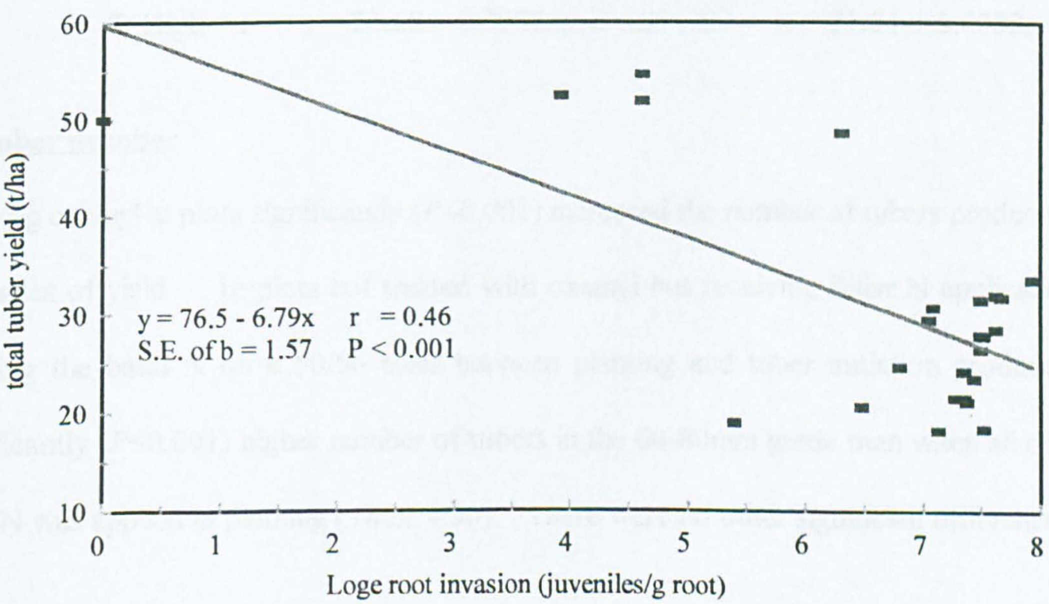

Figure 4.18. The simple linear relationship of $\log_e$ root invasion at 56 DAP on the total tuber yield at harvest (147 DAP) in an investigation of the growth and yield response to oxamyl and basal, tuber initiation and foliar N of potatoes infected by potato cyst nematodes.

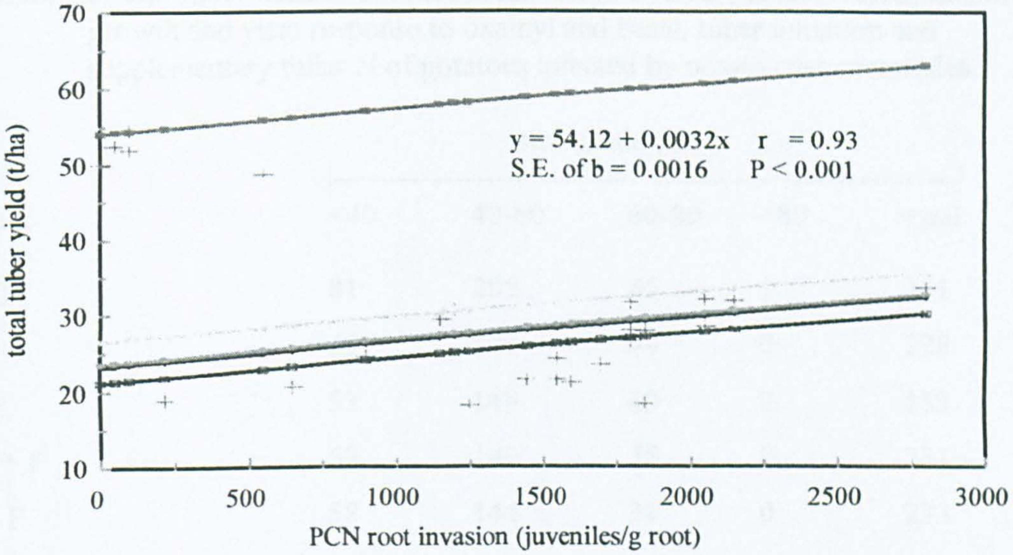

Figure 4.19. Linear relationship (blocked experiment) of PCN root invasion at 56 DAP and the total tuber yield at harvest (147 DAP) in an investigation of the growth and yield response to oxamyl and basal, tuber initiation and foliar N of potatoes infected by potato cyst nematodes.

[a] Regression line parameters :		■ Std + O	y = 54.12 + 0.0032x;
▼ Std	y = 23.34 + 0.0032x;	▲ Std + F	y = 26.60 + 0.0032x
● High + F	y = 23.68 + 0.0032x;	⊠ All + F	y = 21.21 + 0.0032x

iv) Tuber number

Applying oxamyl to plots significantly (P<0.001) increased the number of tubers produced in all grades of yield. In plots not treated with oxamyl but receiving foliar N applications, splitting the basal N on a 50/50 basis between planting and tuber initiation produced a significantly (P<0.001) higher number of tubers in the 60-80mm grade than when all of the basal N was applied at planting (Table 4.30). There were no other significant differences.

v) Tuber dry matter

There were no significant effects of applying all of the basal N at planting or as split applications between planting and tuber initiation, from foliar N applications or from the application of oxamyl to plots at planting (Table 4.31).

Table 4.30. Potato tuber number per plot at harvest (147 DAP) in an investigation of the growth and yield response to oxamyl and basal, tuber initiation and supplementary foliar N of potatoes infected by potato cyst nematodes.

treatment	size grade (mm) <40	40-60	60-80	>80	total
Std + O [b]	81	285	85	1	451
Std	45	140	44	0	228
Std + F	53	149	49	2	253
HIGH + F	53	140	38	0	231
ALL + F	58	144	31	0	233
mean	58	171	49	n.a.[b]	279
overall SED	8.2	16.2	8.1	n.a.	18.5
d.f.	16	16	16	n.a.	16
CV%	22.4	15.0	26.0	n.a.	10.5
<u>Significance (*P* =)</u>					
overall	0.005	<0.001	<0.001	n.a.	<0.001
Std + O vs non oxamyl trts	<0.001	<0.001	<0.001	n.a.	<0.001
Std vs mean of + F trts	n.s.	n.s.	n.s.	n.a.	n.s.
Std + F vs mean High & All	n.s.	n.s.	n.s.	n.a.	n.s.
High + F vs All + F	n.s.	n.s.	n.s.	n.a.	n.s.

[a] see table 4.3.

[b] analysis not applicable (too few values)

Table 4.31. Percentage tuber dry matter at harvest (147 DAP) in an investigation of the growth and yield response to oxamyl and basal, tuber initiation and supplementary foliar N of potatoes infected by potato cyst nematodes.

treatment	dry matter %
Std + O [a]	22.34
Std	21.62
Std + F	22.00
HIGH + F	20.96
ALL + F	21.34
mean	21.62
significance (P=)	n.s.
overall SED	0.688
d.f.	16
CV%	5.0

[a] see table 4.3.

4.5.4 Nutrient status

i) Whole plant at 56 DAP

The percentage N, P and K measured in whole plant dry matter at 56 DAP was significantly (P<0.001) higher in plants from plots treated with oxamyl. An increasing concentration of N was seen with increasing quantities of basal N applied at planting, but only when all the basal N was applied at planting was the increase significant (P<0.001). The high rate of N at planting significantly (P<0.001) reduced the concentration of P below that measured in plants from plots receiving all of the basal N at planting. The K concentration was also shown to be significantly (P<0.001) higher where all of the basal N was applied to plots at planting (Table 4.32).

Table 4.32. Nutrient concentrations of whole potato plant dry matter, at 56 DAP, and potato fourth leaf plus petiole at 107 DAP, in an investigation of the growth and yield response to oxamyl and basal, tuber initiation and supplementary foliar N of potatoes infected by potato cyst nematodes.

	56 DAP			107 DAP		
treatment	%N	%P	%K	%N	%P	%K
Std + O [a]	4.03	0.420	6.92	3.34	0.142	4.10
Std	3.49	0.292	5.49	3.61	0.162	4.23
Std + F	3.50	0.290	5.41	3.84	0.158	4.23
HIGH + F	3.60	0.285	5.54	3.82	0.157	4.26
ALL + F	3.76	0.318	5.78	3.57	0.132	4.13
mean	3.68	0.321	5.83	3.64	0.150	4.19
overall SED	0.078	0.0145	0.133	0.068	0.0057	0.192
d.f.	16	16	16	16	16	16
CV%	3.4	7.1	3.6	3.0	6.0	7.3
<u>significance (*P* =)</u>						
overall	<0.001	<0.001	<0.001	<0.001	<0.001	n.s.
Std + O vs non oxamyl trts	<0.001	<0.001	<0.001	<0.001	0.047	n.s.
Std vs mean of + F trts	0.050	n.s.	n.s.	0.030	0.015	n.s.
Std +F vs mean High & All	0.018	n.s.	0.043	0.034	0.011	n.s.
High + F vs All + F	0.051	0.038	n.s.	0.002	<0.001	n.s.

[a] see table 4.3.

ii) Fourth leaf at 107 DAP

Nutrient concentrations measured in the fourth leaf (plus petiole) at 107 DAP showed that there were no significant differences in the K concentrations between any of the treatments (Table 4.32). Plants from plots treated with oxamyl had significantly (P<0.001) lower N concentrations in their fourth leaf than all plants from plots not treated with oxamyl. Applying all of the basal N at planting resulted in significantly (P<0.001) lower N concentrations than where the basal N was split between planting and tuber initiation, all of which had received supplementary foliar N. Where the normal quantity of N applied at planting was not supplemented by foliar N the N concentration was significantly (P<0.001) lower than where it had been supplemented by foliar N and where a high rate N at planting was used (Table 4.32). Oxamyl application to plots resulted in a significantly (P<0.001) lower P concentration than was measured in plants given normal or high quantities of N at planting. Where all of the basal N was applied at planting, however, this resulted in significantly (P<0.001) lower concentrations of P than were measured in all other plants from plots not treated with oxamyl (Table 4.32).

4.6 General observations and environmental monitoring

The crop protection regime implemented by the grower was successful in all aspects as no weeds, diseases or pests (other than PCN) which would have been detrimental to crop performance were seen in the experiments. The soil moisture deficits, recorded every seven days, were maintained at a maximum of 30 mm (figure 4.20) by irrigation, with the grower utilising the neutron probe readings from the experiments to plan the irrigation scheduling. Soil temperatures, logged at 20 cm depth within a potato ridge, were monitored throughout the growing season with a Tinytalk® soil temperature data logger. The complete data set of 1394 readings are available but the basic information is as follows: a minimum soil temperature of 5.3 °C at 28 DAP, a maximum soil temperature of 28.3 °C at 133 DAP, and an average soil temperature of 15.8 °C. The air temperature was monitored at 45 cm above the potato ridge with a Tinytag® air temperature data logger. A total of 6394 readings were logged, with a minimum recorded temperature of -1.4 °C at 28 DAP, a maximum of 34.4 °C at 133 DAP, and an average of 15.4°C. The precipitation was recorded at the experimental site with an ELE International Rain-o-matic® raingauge. The total recorded for the whole of the experimental period was 370 mm of precipitation. This included both natural rainfall and irrigation.

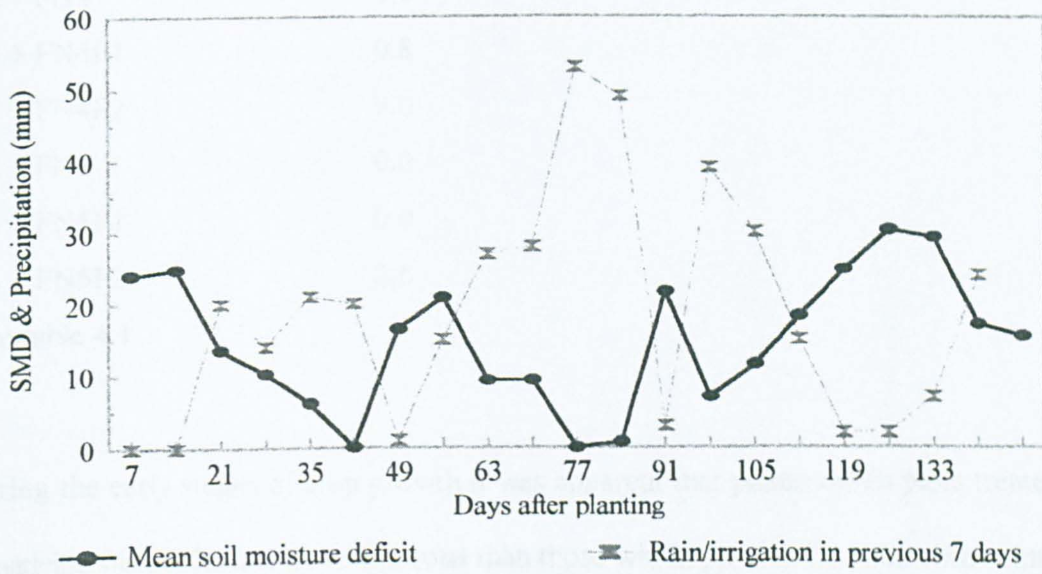

Figure 4.20. Mean soil moisture deficits and precipitation, taken at seven day intervals, in the investigations of the growth and yield response to oxamyl and fertiliser applications of potatoes infected by potato cyst nematodes.

Two days after the application of the first foliar treatments (70 DAP) the foliage of experiment one was assessed for leaf injury resulting from the applications. The results were not analysed statistically due to the high frequency of zero scores. The observations showed that where foliar P had been applied at 3.4% P, without foliar N, a much higher level of scorch existed than where 3.4% P had been applied with foliar N. Where foliar P had been applied at 1.7% P without foliar N only slight damage was seen. The 1.7% P application with foliar N showed no sign of scorch (Table 4.33). The relevance of leaf damage is discussed further in the discussion and conclusions section.

Table 4.33. Levels of foliage scorch recorded two days after the first foliar nutrient

applications (70 DAP) in an investigation of the growth and yield response to oxamyl and supplementary foliar N and foliar P of potatoes infected by potato cyst nematodes.

treatment	% necrosis of green leaf area
Std + O [a]	0.0
Std + FN4	0.0
Std + FN4P1	0.8
Std + FN4P2	9.0
Std + FN5	0.0
Std + FN5P1	0.0
Std + FN5P2	2.6

[a] see table 4.1

During the early stages of crop growth it was apparent that plants within plots treated with nematicide were taller and more vigorous than those within plots not treated with nematicide. At 66 DAP, plants in nematicide treated plots appeared to be lighter green than the plants within non-nematicide treatments. At 84 DAP purple leaf discolouration was seen on random plants but was not associated to any individual treatment. At 91 DAP, a dark brown 'speckling', classed as discolouration, appeared on plants within the non-nematicide treatments which, when assessed, was shown to be treatment related (Table 4.8) and is expanded upon in the following discussions.

4.7 Discussion

In the following discussions the treatments are referred to by the abbreviated forms used in the tables of results. Although this may require that the reader refers to treatment descriptions occasionally, the explanations and discussions become far easier to follow when written in this way. Two treatment descriptions which remain constant through all three experiments;

'Std (control)' this is the standard fertiliser practice with no other fertilisers applied and NO oxamyl application (therefore representing a base level of PCN infection and providing a standard from which to measure yield and tolerance).

'Std + O (control)' the standard fertiliser practice with no other fertilisers applied but WITH oxamyl applied to the plots at planting (producing a yield and tolerance level as close as possible to the yield and tolerance expected in a PCN free soil).

4.7.1 PCN population studies

The initial PCN population densities in all three experiments were not significantly different between treatment means, suggesting that no one treatment would be under more or less PCN pressure than any other. The ranges of populations were, however, quite large with coefficients of variation between 30 and 34.7%. The development of PCN infestations from foci within fields, however, makes it very difficult to obtain homogenous PCN populations across an experiment. The final population densities were significantly reduced in all three experiments from a mean of 86 eggs/g soil down to a mean of 8 eggs/g soil. This reduction was reflected in the mean Pf/Pi value of 0.08. The ability of oxamyl application to reduce population densities of *G. rostochiensis* and *G. pallida* and achieve Pf/Pi ratios as low as 0.1 has been shown by Whitehead *et al.* (1984) and Trudgill *et al.* (1983) but such excellent control is not usual. Since Pf/Pi ratios were also low in plots not treated with oxamyl, however, the decrease in population density must have been mainly due to the full PCN resistance of the cultivar to *G. rostochiensis* plus its partial resistance to *G. pallida* (Anon, 1997) which, in this instance appears to have been very effective. Hancock (1994) and Gurr (1987) demonstrated the ability of the cultivar Santé to reduce populations of *G. pallida,* both with and without nematicide, but attained Pf/Pi ratios of 1.69 and 0.93 respectively. As the Pf/Pi's from the experiments in this thesis were consistently less than 0.1 (in plots not treated with oxamyl), the findings suggest that although both *G. rostochiensis* and *G. pallida* were identified within the experiments, the population was predominantly *G. rostochiensis*.

4.7.2 Root invasion

The effectiveness of oxamyl in reducing the number of PCN juveniles/g root, sampled at 56-61 DAP, was clearly demonstrated in all three experiments. Although the application of oxamyl to the plots at planting did allow some PCN invasion of the plant roots it was at a very low level (0-250 PCN juveniles/g root). The growth and yield of plants from these plots should, therefore, have provided an effectively PCN-free base from which to compare the growth and yield response of the PCN-infected plants within the experiments. Such information is very important for ascertaining the performance of non PCN-infected plants, and the tolerance and response to any treatments applied to PCN-infected plants in a specific environment (Evans and Franco, 1979).

In the foliar N/foliar P and the rate of foliar N experiments, no foliar treatments had been applied when the root invasion samples were taken, so no effects of foliar treatments would be expected. In the basal, tuber initiation and foliar N experiment the application of increased quantities of fertiliser N applied at planting, rising from 120 to 240 kg N/ha, produced no significant effects on the number of juveniles in the roots. The plots receiving the higher rates of N at planting (180 and 240 kg N/ha) did, however, have fewer PCN juveniles/g root than were found in plants from plots receiving 120 kg N/ha in the seedbed. As Sudirman & Webster (1995) have shown that high levels of ammonium ions slow down or inhibit invasion of tomato (*Lycopersicom esculentum* Mill.) roots by *Meloidogyne incognita,* the larger applications of the ammonium nitrate fertiliser used in the experiment could have slowed down or inhibited invasion of potato roots by PCN.

4.7.3 Plant emergence

The emergence assessments were carried out over a 16 day period, from 33 to 49 DAP, after an initial assessment at 28 DAP to gauge when emergence was likely to begin. The oxamyl treatment showed significant benefits for crop emergence in all three experiments at 33, 35 and 37 DAP and also at 40 DAP for the foliar N/foliar P and basal N experiment. By 42 DAP there were no benefits of oxamyl on emergence and all plants had emerged by 49 DAP. The nematicide could be judged to have improved emergence *per se* but, as its main role is to control PCN and prevent root invasion, it is more likely that the PCN invasion in the non oxamyl treated plots (see section 4.7.2) significantly retarded the emergence of the plants. This agrees with Van der Wal (1978), who showed that infection of potatoes by PCN slows plant growth in the first few weeks. The reason for this delayed emergence could be changes in the mineral nutrition of the pre-emerged plant which, although still depending on the mother tuber for much of its nutrition, forms roots which increases the supply of mineral ions (Moorby and Milthorpe, 1975). The normal increase in nutrient uptake then increases both the rate of emergence and number of stems appearing above the ground (Moorby, 1968). Where the roots are damaged by PCN invasion, however, a reduction in the uptake of minerals in the very early stages of plant growth could delay plant emergence. The levels of invasion recorded in the experiments were similar in most instances to those given by Evans (1969), who reported that roots are invaded before emergence and recorded PCN invasion of more than 2000 juveniles per g root at 60% crop emergence (33 DAP).

4.7.4 Ground cover

Ground cover assessments, which relate to the amount of intercepted radiation, are considered by Haverkort and Schapendonk (1994) as one of the most suitable techniques to measure stress in PCN infected plants. For this reason ground cover assessments were carried out on a regular basis within these experiments. These ground cover measurements showed that the early benefits of oxamyl on plant emergence continued and significantly higher percentage ground cover was maintained from 49 to 120 DAP. In all three experiments, plants in oxamyl treated plots had achieved 100% ground cover by 76 DAP and this was maintained until 120 DAP, at which point ground cover declined rapidly to become significantly lower than other treatments at 146 DAP. This progression of ground cover follows the normal growth and senescence pattern of a non-PCN-infected crop. The plants in plots not treated with oxamyl never achieved greater than 75% ground cover at any point in the season and this declined shortly after the plants from oxamyl treated plots. These findings are similar to those of Trudgill *et al.*(1975a) where the percentage ground cover was less in plants infected by PCN but, unlike Trudgill's plants which senesced earlier in the season, the plants in these experiments senesced later as seen by Seinhorst & Den Ouden (1971).

In the foliar N/foliar P experiment the foliar nutrient application programme was initiated at 68 DAP. The percentage ground cover at 76 DAP showed low values from the foliar application of 3.4% P, in the four N spray regime (FN4P2), which could have caused reductions in plant growth as shown by Okuda & Yamada (1962). This treatment also caused up to 10% leaf damage by only two days after nutrient application. Foliar P at this concentration, equivalent to 10.2 kg P_2O_5/ha, was shown by Barel & Black (1979a) to cause leaf damage on soyabean (*Glycine max* L. Merr.) and corn (*Zea mays* L.). The solution was, however, very acidic (pH 1.8) and this could have been the main cause of the damage as Barel & Black (1979b) also showed that leaf damage was severe at high P concentrations of pH 2.0. Barel & Black (1979b) also show that over the range of pH 2 to 10 there was no detrimental effect on the absorption and translocation of the foliar P, which exceeded 90% at most application rates. Barel & Black (1979b), also noted scorch in soyabean and corn at only 2.74

kg P_2O_5/ha with the addition of urea. This was not the case in my experiment, where the 3.4% P application was made in a 4% urea solution and little or no leaf damage was seen. The differences in leaf damage observed by myself and Barel & Black (1979b), with or without foliar urea, may be accounted for by differences in the composition or quantity of the epicuticular waxes between the plant species studied, as found between potato cultivars (Lewis, 1994). The early season ground cover, up to 104 DAP, appeared to benefit most from the five foliar N applications, at both levels of foliar P, and the four foliar N treatments plus the 1.7% P applications, whereas the 120 and 133 DAP ground cover assessments suggest that only the five foliar N alone and the five foliar N plus 1.7% P benefited ground cover. The early ground cover would benefit from applications which included P (Watson & Wilson, 1956), whereas applications of foliar N would increase leaf and stem growth (Dyson & Watson, 1971) and benefit leaf area duration (Millard & Marshall, 1986). There were no plots in this experiment which were a Std (control) to judge any potential benefits to ground cover from foliar nutrients. The mean percentage ground cover for the season was calculated to identify whether any one treatment had maintained a significantly higher or lower overall percentage ground cover. Plants in the Std + O (control) plots had significantly greater ground cover but there were no other significant differences. This suggests that, although foliar applications resulted in small improvements in individual assessments of ground cover, there were no accumulated benefits over the whole growing period.

In the rate of foliar N experiment, applications of foliar N showed small non-significant improvements to the ground cover from 76 to 104 DAP. By 120 DAP only the 6% foliar N application still retained greater ground cover than the Std (control). There was almost a significant linear (P=0.051) improvement in ground cover at 76 DAP to increasing rates of foliar N. This would suggest that the first application had been made at a time when plant demand for N was exceeding its uptake from the soil, thus redressing a deficiency and promoting plant growth. The lack of effects later in the season could have arisen if the internal nutrient concentration of the plant, which regulates uptake (Clement *et al.*, 1978), was at a sufficient level. When the nutrient concentrations were determined at 98 DAP it was shown that the N concentrations were much higher in plants which had been treated with foliar N applications (section 4.4.4.ii) lending weight to this argument. If other factors had become limiting after 76 DAP then the supplementary foliar N would not benefit crop growth due to the limits imposed by the secondary limiting factor (proposed by Liebig in (Mengel & Kirkby, 1987). Such a limiting factor could have been the amelioration of other nutrients. Consideration of nutrient concentration is made later in these discussions.

In the basal, tuber initiation and foliar N experiment there were no benefits to early ground cover from increased N applications at planting. Therefore the hypothesis that "increasing the N quantity at planting may stimulate early growth of PCN infected plants " was found to be discredited. Growth to plants where all of the fertiliser N was applied in the seedbed at planting and foliar N applications were also made (ALL + F), was initially on a par with the Std (control) but, by 104 DAP, these plots had significantly less ground cover than both the Std (control) and the Std +F. This trend continued with very significant reductions in ground cover in the ALL +F treatment. This suggests that N uptake from the roots is an important aspect of the nutrition of a potato plant with a PCN-damaged root system. Without the application of N at tuber initiation, applying all of the N (240 kg N/ha) at planting, on a well irrigated crop on a light soil, probably led to leaching of the N. This would agree with the findings of Gunasena and Harris (1971) who suggest that beneficial effects from split applications of basal nitrogen may arise from reduced N loss through leaching. However, when the fertiliser quantity was split 50/50 between planting and tuber initiation, the use of foliar N to supplement the supply from the roots did little to promote additional ground cover. This may suggest that N was not deficient throughout the season as the crop response to the additional fertiliser was minimal, as would be expected where the N supply was adequate (Neeteson, 1989).

One of the hypotheses of these experiments was that supplementary foliar nitrogen and foliar phosphate could improve the ground cover and LAI and thus increase the tolerance and yield of PCN infected plants. The ground cover improvements were small and non- significant at most of the assessment times. The cultivar used in these experiments may have been unable to respond to the supplementary nitrogen as the determinate nature of the cultivar may have prevented further leaf growth (PMB, 1993). In a discussion with the breeder of this cultivar, Agrico Holland of Cambridge, UK, the determinate nature of Santé could not be ascertained as it was not a trait that they record.

4.7.5 Plant fresh and dry weight

The plants from plots treated with oxamyl were shown to be significantly heavier than all plants from plots not treated with oxamyl. This emphasises the benefits to earlier emergence and achievement of rapid growth of freeing plants from PCN infection. In the basal, tuber initiation and foliar N experiment, increasing the quantity of N applied at planting did not benefit the plant weights. These results are therefore similar to those of the field experiments of Trudgill (1980), where no benefits to the haulm were found from increased quantities of fertiliser N at planting.

4.7.6 Leaf discolouration

The leaf discolouration was first seen at 91 DAP and was assessed in the rate of foliar N experiment. The only difference found was that plants in plots treated with oxamyl showed no signs of the discolouration whereas all of the plants in plots not treated with oxamyl had 3.4 to 4.0% discolouration. The brown speckling symptoms were similar to those shown and described by Hewitt (1983) and Westermann (1993) as K deficiency in potatoes. Leaf sample analysis, however, suggested that the K concentrations were approximately 4.2%. As concentrations of greater than 3.5% are though to be adequate for unrestricted growth at this sampling time (Reuter and Robinson,1986; Walworth and Muniz, 1993; Westermann, 1993), K deficiency was unlikely to be the cause of the leaf discolouration. Visual symptoms of Mg deficiency are similar to those of K deficiency, in that a dark brown speckling or discolouration occurs. This was also a possibility as Trudgill *et al.* (1975c) had already shown that concentrations of Mg are reduced by PCN infection. This was considered unlikely, however, as the discolouration was not interveinal and no chlorosis was seen (Hewitt, 1983). In addition, the chlorosis associated with Mg deficiency, caused by a reduction in chlorophyll production, would have been detected when the chlorophyll levels were measured and no chlorophyll deficiency was recorded. Leaf discolouration was also assessed in the foliar N/foliar P experiment, at 99 DAP. The plants in oxamyl treated plots showed some discolouration but this was significantly less than all other treatments. Statistical analysis showed significantly less ($P = 0.001$) discolouration in treatments containing foliar P than was seen in treatments without foliar P. Further evidence for the influence of P was seen when the analysis showed that applications containing 3.4% P resulted in significantly less (P=0.001) discolouration than those containing 1.7% P. These observations suggest, therefore, that the discolouration was P related which, adds weight to observations throughout the season where plants from oxamyl untreated plots were a much darker green throughout the whole growing period. This is consistent with both Hewitt (1983) and Perrenoud (1983), who suggest that P deficiency can result in dark-green, stunted plants. The results of the chlorophyll measurements also concur with Rao and Terry (1989), who concluded that higher chlorophyll levels in leaves of P deficient plants cause the darker green foliage.

4.7.7 Leaf injury (scorch)

One of the consequences of applying foliar N and P to plant tissue is their tendency to cause damage to the leaf at relatively low nutrient solution concentrations (Gray, 1977). This leaf damage is seen in the form of a localised leaf tissue necrosis, known as 'leaf burn' or 'scorch', which is undesirable as it reduces the photosynthetic area of the leaf and therefore dry matter production. The amount of leaf injury will vary depending on the nutrient applied, the nutrient source, e.g. ammonium N or urea N, and the concentration of the nutrient in solution. There are several theories regarding the cause of leaf damage. Neumann (1987) suggested that leaf necrosis arising from applications of foliar nutrients was due to a higher salt concentration in the foliar nutrient droplets than found in the plant cells, thus causing a loss of water from the plant cell by osmosis, followed by plasmolysis, and localised cell death. Marschner (1995), however, disagrees with the plasmolysis theory and suggests that the leaf damage is the result of local nutrient imbalance within the leaf tissue. As yet, no definitive explanation exists for the causes of the leaf damage but methods such as the inclusion of urea, sucrose and glycols in solutions for foliar application have been investigated (Barel and Black, 1979b) for their potential to reduce the severity of the problem.

In the experiment that investigated the effects of foliar N and foliar P on the growth and yield of PCN infected plants, leaf damage was assessed as the percentage of the green leaf area showing necrosis. Foliar N applied alone at 4% showed no adverse effects on the leaf tissue. Phosphate applied alone at 1.7% showed only minimal damage, whereas P applied alone at 3.4% showed 10% loss of green leaf area to necrosis. When P was applied with the 4% urea solution, however, no damage was seen with 1.7% P and a much smaller reduction of green leaf area was seen with the 3.4% P application.

4.7.8 Chlorophyll content

Chlorophyll content was measured 66, 84, 98, 112, 119 and 133 DAP. The plants from oxamyl treated plots showed significantly lower chlorophyll content than all other treatments at 66, 84, 112, 119 and 133 DAP. The Std (control) treatment maintained similar chlorophyll contents to treatments receiving foliar N up to 119 DAP, after which time it contained significantly less than any foliar N treatment. There was a significant difference between the foliar treatments at 133 DAP, when the 4% foliar N treatment had significantly less chlorophyll than the 6% foliar N treatment. The assessments at 112 and 119 DAP demonstrated a significant linear increase in chlorophyll content with increasing rates of foliar N. A relationship between the chlorophyll content of leaves and the Mg and N status of the plant exists because both elements are primary constituents of the chlorophyll molecule, Mg being the central element of a complex structure (porphyrin ring) which is attached to four N atoms. When plants are deficient in Mg and/or N, chlorophyll production is restricted and chlorosis occurs. The use of the hand held chlorophyll meter to assess the N status of plants was demonstrated by Vos and Bom (1993) who attained a correlation of $r^2>0.95$ between meter readings for chlorophyll and laboratory measurements of chlorophyll and N contents. The results of the chlorophyll readings would suggest, therefore, that neither N nor Mg were deficient in the PCN infected plants, as they always contained more chlorophyll than the plants from oxamyl treated plots, which were growing well. There is evidence suggesting that P deficient plants can contain higher levels of chlorophyll than plants with no P deficiency, because leaf expansion is restricted by an inadequate P supply whilst the production of chlorophyll is not, giving plants with very dark green leaves (Rao and Terry, 1989), as observed in these experiments.

4.7.9 Tuber dry matter

The dry matter was measured at harvest (147 DAP) to identify whether the application of the supplementary foliar nutrients or the rate of N at planting had affected this tuber quality measurement. Tuber dry matter content was significantly higher in tubers from plots treated with oxamyl than where tubers came from oxamyl untreated plots, in both the foliar N/foliar P and the rate of foliar N experiments. None of the foliar nutrient treatments or increased quantities of N at planting significantly affected tuber dry matter content. However, the mean tuber dry matter contents were 21.3% for all tubers from oxamyl untreated plots and 22.2% for tubers from oxamyl treated plots, suggesting that tuber dry matter is not greatly affected by PCN infection of potato roots.

4.7.10. Tuber yield

The treatment of plots with oxamyl showed significant benefits to the crop yield in all three experiments, underlining that no other individual treatment had improved yield to anywhere near that of oxamyl treated plots. The rate of foliar N and basal, tuber initiation and foliar N experiments both contained a Std (control) treatment and none of the nutrient treatments proved significantly better than this control. In the basal, tuber initiation and foliar N experiment, where the quantity of N applied at planting was the same as the Std + O (control), the addition of the five 4% foliar N applications did increase the total tuber yield by 3.42 t/ha. This increase in yield could be attributed in part to the small increases in ground cover, shown in the mean percentage ground cover for the season (section 4.5.2.ii), which would increase dry matter production (Millard & Marshall, 1986). The actual yield increase was attained from a greater number of tubers in the 40 to 80 mm grades.

Where the total N was split 180 kg N/ha at planting and 60 kg N/ha at tuber initiation, accompanied by five 4% foliar N applications, the yield was less than the Std (control) treatment. Where all of the N was applied at planting, and this was followed by five supplementary 4% foliar N applications, the total tuber yield was reduced by 2.8 t/ha relative to the Std (control) and by 6.2 t/ha relative to the Std +F treatment. This trend was reflected by a lower tuber number in the ALL +F than was recorded for the Std +F treatment. It is possible that the number of tubers initiated were similar but that lack of adequate nutrition caused a re-absorption of the tubers as the season progressed (Gunasena, 1969). One of the problems associated with the use of high rates of N at planting is that a delay in tuber initiation itself can occur, which can in turn result in a reduction in the overall tuber growth and yield, arising from delayed plant maturity (Anon, 1993). Applications of all or the majority of the total recommended N at planting can also result in high N leaching losses, especially on light free draining soils and especially under well irrigated crops (Gunasena and Harris, 1969; 1971). For this reason alone it is beneficial to split the application of the nitrogen between planting and tuber initiation. Where roots are also damaged by PCN, early season nitrate losses could increase, as Millard and Robinson (1990) suggest that in the absence of an active root system nitrates may be lost through leaching, denitrification or immobilisation in the microbial biomass. Thus, splitting the total N requirement between planting and tuber initiation may be essential for maintaining the concentration of N in soil solution at a level that the smaller, PCN-damaged root system is able to utilise.

The foliar N rate experiment showed no significant differences between non oxamyl treated plots. The 4% and 6% foliar N treatments did increase the total yield over that seen in the Std (control), however, by 3.84 and 4.8 t/ha respectively. This was reflected by a significant linear response to the rate of application of foliar N in the 40-60 mm grade and small benefits to the ground cover through the season. An explanation for this trend can be seen in the numbers of tubers produced by increasing quantities of foliar N. In both the 40 to 60 mm grade and the total numbers of tubers, there were significant linear increases ($P = 0.029$ and $P = 0.015$ respectively) in the numbers of tubers harvested. The increased yields of both the 4% and 6% foliar N treatments arose, therefore, from a higher number of tubers harvested. This would suggest that, as foliar applications commenced during tuber initiation, the resulting increased nitrogen nutrition of the crop was beneficial in either increasing the numbers of tubers formed or preventing the re-absorption of those formed and providing adequate nutrition for their growth. Millard and Robinson (1990) also report that late applications of foliar urea, in the absence of PCN, can result in increased yields, but that increases are inconsistent and only found with long growing seasons.

In both the basal, tuber initiation and foliar N and the rate of foliar N experiments, the small tuber yield increases from the five 4% foliar applications may be indicative of an essential characteristic of PCN-infected plants. As previously discussed, the feed-back mechanism associated with a sufficient supply of N (Clement *et al.*, 1978) may well indicate that the PCN-infected plants in these experiments were not suffering greatly from N deficiency. This would be substantiated by the yield response to the supplementary foliar applications, in addition to the 240 kg N/ha broadcast granular application, which would be negligible in plants not infected with PCN (Neeteson, 1989). Therefore, if plant growth had been restricted by N deficiency, removal of the limiting nutrient should have given a more substantial yield response.

In the foliar N/foliar P experiment there was no non-oxamyl control and this has led to difficulties in determining any tolerance or yield benefits arising from the experiment. The results from this experiment still showed a significant yield benefit from the use of the oxamyl. There were no significant differences between any of the foliar treatments. The highest yields were seen from five 4% foliar N applications with one 3.4% P application in the first foliar N application (29.5 t/ha), and when one early 1.7% P application was followed by four 4% foliar N applications (28.6 t/ha). These yields were similar to those seen from a five spray 4% foliar N application in the basal, tuber initiation, foliar N and foliar N rate experiments. However, the same five spray 4% foliar N in the foliar N/foliar P experiment achieved only 23.97 t/ha, suggesting that both the 4% foliar N applied in a five spray programme with the addition of the one early 3.4% P application and the 4% foliar N in a four spray programme with the addition of one early 1.7% P application may have increased the yield well above that of a Std (control) treatment. These same treatments also produced the highest total tuber number and highest number of ware grade tubers, indicating that the treatments either increase the number of tubers set or provide sufficient nutrition for those set to grow, as shown by Lewis (1994).

The poor yield recorded by the four 4% foliar N plus one 3.4% P application was probably the result of the early loss of photosynthetic leaf area due to scorch. The potential for an early application of foliar phosphate to increase yields has been shown by several workers. Johnson and Vaidyanathan (1993) reviewed the results of 49 experiments and concluded that applications of foliar phosphate can increase tuber yields when applied in addition to the recommended quantities of basal fertiliser. Lewis (1994) reported 5% yield increases where foliar P was applied at tuber initiation in addition to a basal soil application of 100 kg P/ha. It was also reported that a 4% increase in total tuber number occurred but that tuber counts earlier in the season had recorded greater numbers, which led to the conclusion that some of the tubers were re-absorbed where P or N concentrations had been insufficient to maintain all of the tubers initiated.

As the amount of photosynthetically active radiation intercepted by the crop has a direct positive relationship with potato tuber yield (Harris, 1992), a comparison of the yields and mean percentage ground cover over the season would be expected to show greater yields where there was greater ground cover. It can be seen, however, that the highest yields of non-oxamyl treatments do not always correspond to greater ground cover, suggesting that yield improvements were not from ground cover improvements in this experiment.

i) Covariance analysis and yield

The yields of all three experiments were also analysed with covariates. However, the use of covariance in statistical analysis must be considered carefully as there are underlying principles that must be taken into account. Gomez and Gomez (1984) list three constraints for its use: 1) where covariance is used for the control of error then the covariate must not be influenced by the treatments being investigated; 2) if the covariate is used to adjust treatment means then it should not be affected by the treatments being investigated; and 3) if the covariate is used to aid the interpretation of results then the covariate must be closely associated with the treatment effects. The use of covariance in these experiments was to adjust the treatment means so that the effects of all treatments could be assessed at a uniform level of PCN infection, and therefore falls into the second category. It might be expected that the normal covariate to use in PCN experiments would be the initial PCN population densities but, there are two problems with this approach. Firstly, although there is a substantial body of evidence to show a strong correlation between initial PCN population densities and potato tuber yield, Brown (1983) found that the initial populations were not always strongly related to yield. Secondly, these nutrient experiments utilised a nematicide to reproduce, as closely as possible, the effect of a PCN free soil and the nematicide should have reduced the numbers of live hatched PCN from the treated area. The result of this would be to lower the effective initial population density below that attained during sampling and would reduce its relevance as a covariate as the PCN pressure would no longer be related to the recorded initial population. This is shown in these experiments by the much reduced number of juveniles/g root found in plants from plots treated with oxamyl, 0 to 250 juveniles/g root, as opposed to the 4,500 juveniles/g root found in plants from oxamyl untreated plots. Therefore, although covariance analysis was performed using Pi and shown in the results, it is suggested that this particular adjustment of treatment means is inappropriate. A second covariate possibility was to utilise the level of PCN infection as quantified by root invasion. Evans, Trudgill and Brown (1977) and Trudgill *et al.* (1975a, 1975b) show that PCN root invasion (juveniles/g root) is related to crop yield, as invasion increases the yield decreases in the majority of cases. Their data, however, were presented without analysis of any linear relationships or any assessments of the suitability of invasion data as a covariate.

ii) Regression analysis of tuber yield

As no information was found in the literature to demonstrate a definite relationship between PCN root invasion and yield, it was necessary to identify whether a relationship could be seen in the nutrient experimental data. The regression analysis of blocked experiments, however, requires that the data is grouped into treatments and blocks first and then analysed for any significant interactions of the treatments and invasion. If an interaction is shown, then the data would be unsuitable for demonstration of linear relationships of root invasion and yield because the treatments would be affecting invasion. Although any foliar treatment effect on invasion would be unlikely, as the treatments were applied after the root invasion analysis and could not therefore have influenced the invasion, the principles of the analysis required the proof. In the case of the rate of N at planting experiment, the treatments could have influenced the invasion and the regression technique would be entirely appropriate. The results of the regression analysis suggest that a relationship between PCN root invasion and yield does exist in one out of the three experiments. The foliar N/foliar P experiment showed a significant relationship, with lower yields resulting from increased root invasion. The results from the rate of foliar N experiment suggest that no relationship exists but that there is still a negative trend, whereas the results from the rate of basal N experiment also show no relationship but suggests a positive trend of invasion on yield. The results of these latter two experiments, showing a non-significant relationship, are possibly best interpreted without covariance analysis, whilst the results of the foliar N/foliar P experiment can be interpreted with an invasion covariate. A comparison of the results for this experiment without covariance and with invasion covariance show that the highest yielding non-oxamyl treatments are still the 4% foliar N applied in a five spray programme with the addition of the one early 3.4% P application and the 4% foliar N in a four spray programme with the addition of one early 1.7% P application. The five 4% and four 4% foliar N applications without foliar P treatments also show appreciably higher yields in the covariance analysis.

The differences seen in the relationships between the three experiments may have been influenced by the actual timing of root invasion sampling but, as the timings were within five days of each other (56-61 DAP), this is doubtful. However, the root invasion data for the basal, tuber initiation and foliar N experiment, which demonstrated a positive trend, could have been influenced by the quantity of N applied at planting for the reasons discussed earlier (i.e. high levels of ammonium ions slow down or inhibit invasion of tomato by *Meloidogyne incognita*).

4.7.11 Plant nutrient status

i) 56 to 61 DAP

The plant nutrient status was first measured before the application of foliar nutrients; in the foliar N/foliar P experiment at 61 DAP; in the rate of foliar N experiment at 58 DAP and in the basal, tuber initiation and foliar N experiment at 56 DAP. In all of these experiments the concentrations of N, P and K within whole plant dry matter were significantly lower in plants from oxamyl untreated plots. Defining these concentrations as deficient or sufficient by comparison with published values, however, was not sensible, as the published values for whole plant nutrient concentrations (Walworth & Muniz, 1993) were single values (e.g. 4.2 %) and not a range of values (e.g. 3.5 to 4.5%), and thus too rigid. As the effect of the oxamyl application on PCN was shown to be a significant reduction in the number of PCN juveniles invading the roots at 56-61 DAP (section 4.7.2), the direct relationships between the nutrient concentrations and PCN invasion were investigated. The results of simple linear regression showed that, in the foliar N/foliar P and rate of foliar N experiments, the N, P and K concentrations were reduced by increasing numbers of PCN juveniles counted in the potato roots with r^2 values of 0.68 & 0.79 for K, 0.49 & 0.67 for P and only 0.18 & 0.36 for N. However, as the use of simple regression models is not strictly applicable to blocked experiments, these relationships were also investigated with a method of regression analysis designed for blocked experiments. The results of this analysis followed the same trend as the simple regression with the relationships best described by K, r^2 = 0.68 & 0.87, followed by P, r^2 = 0.66 & 0.78, and the poorest relationship with N, r^2 = 0.50 & 0.51. From these results it is possible to suggest that during this early phase of plant growth the significant reduction of plant nutrient concentration is related to the level of root invasion by PCN, with K and P being most affected. These findings are not conclusive but do correspond to some of the previous research in this area. Trudgill *et al.* (1975a) showed that at similar levels of root invasion (>2000g/root) only slight decrease in %N in haulm was found during the early growth of the crop, but decreases in %K were high. Trudgill *et al.* (1975b) concluded that, on a dry matter basis, concentrations of N, P, K and Mg were all decreased in PCN-infected plants. On a fresh weight basis, however, only K and P concentrations were decreased and the decreases were less in a cultivar tolerant of PCN attack. Van Oijen *et al.* (1995) reported that concentrations of N, P and K were all reduced in one year but much less so in a second year. In experiments with increased rates of fertiliser, Trudgill *et al.* (1975c) report that concentrations of N, P and K were decreased little by nematode infection, except for %K in the cultivar Record and where plots were treated with standard and one and a half times the standard rate of N, P and K, where the concentration of P was decreased. It was also reported that in field experiments where four rates of N, P and K fertilisers were used (1x, 1.5x, 2.0x and 2.5x the standard rates) the concentration of K in plants was largely unaffected by PCN infection and that N concentration, although lower at the lower rates, was not significantly affected.

To further determine the effect of the PCN induced reductions of N, P and K concentrations, the relationships of the nutrient concentrations to final tuber yields in the experiments were analysed. The simple linear regression of nutrient concentrations and final tuber yields followed the same patterns as the root invasion effects and nutrient concentrations. The K and P concentrations were both well related to tuber yield, showing that higher concentrations of these nutrients were linked to higher tuber yields. Where the blocked experiment regression analysis was used, there were similarly strong relationships for N, P and K concentrations, again with increasing concentrations linked to greater tuber yields. Therefore, it seems that the effect of invasion of potato roots by PCN is initially to cause reductions in N, P and K concentrations, which then result in corresponding reductions of final tuber yield, which also agrees with the findings of Trudgill (1980, 1987).

The basal, tuber initiation and foliar N experiment also showed significant reductions in N, P and K concentrations in whole plant dry matter, at 56 DAP, resulting from root invasion by

PCN. One of the experiment aims was to determine the effects of increasing the quantity of seedbed N on the nutrient concentration in the plant. As might be expected, increasing the quantity of N (and thus the availability of N) at planting, gave rise to significant increases in the whole plant N concentration. However, there were also corresponding increases in the whole plant concentrations of P and K. This is not an unusual response as Trudgill (1980) reported that increasing the quantity of any one element (N, P or K) applied, greatly increased the total uptake of all three elements and also increased root size. The most widely held concept as to why potato root invasion by PCN causes the reductions in concentrations of N, P and K is a reduction in plant root growth. Trudgill (1980) and Evans *et al.* (1977) have both shown that root invasion by PCN can severely reduce root growth, which subsequently leads to a reduction in nutrient uptake. For both P and K uptake it is essential for the roots to explore a sufficient soil volume as nutrient acquisition depends mainly on the diffusion mechanism (Barber *et al.*, 1963; Mengel & Kirkby, 1987). This may explain why N has seldom been found to be the most limiting in PCN infected plants, as N is transported through soils by mass flow and reductions in root growth would therefore not be so restrictive to N uptake. Root system size was not measured in the basal, tuber initiation and foliar N experiment, but increases in root size would lead to a greater nutrient uptake potential and could be the reason why all three nutrient concentrations were increased in this experiment. The form of N fertiliser can also influence the uptake of other nutrients. Where fertiliser N is in the form of NO_3^-, the soil pH is raised and the absorption of cations, especially K, is enhanced. Where fertiliser applications are in the form of NH_4^+, the rhizosphere pH is lowered by root excretions of H^+ in response to ammonium absorption. This promotes the conversion of soil $H_2PO_4^-$ to the more rapidly absorbed HPO_4^{2-} (Lewis, 1986) which promotes anion absorption and in particular phosphates. It is doubtful, however, that both of these effects could occur at the same time, when the fertiliser N application in this experiment was a combination of ammonium and nitrate ($NH_4^+NO_3^-$).

<u>**ii) 98 to 107 DAP**</u>

In all three experiments the nutrient status was measured in the dry matter of the fourth leaf from the top of the plant, at 98 DAP in the foliar N rate experiment, 104 DAP in the foliar N/foliar P experiment, and 107 DAP in the basal, tuber initiation and foliar N experiment. The nutrient concentrations were all significantly higher in plants from plots not treated with oxamyl. This is in contrast to most of the reports of potato plant infection with PCN but the majority of reports relate to plant analysis at earlier times. A noteable exception is Trudgill *et al.* (1975c) where concentrations of N, P and K in leaves sampled in August (approx 118 DAP) were decreased little by PCN infection, except for %P in the cultivar Pentland Crown. Work by de Ruijter (1998), however, whose results included samples taken at 116 DAP, did show some instances where both N and P concentrations were higher in nematode infected plants. This inverted nutrient concentration response to PCN infection could be related to a proliferation of roots during the later stages of crop growth, as shown by Haverkort *et al.* (1994), which would enhance the ability of the plants to take up nutrients from the soil. The natural nutrient concentration pattern of the plants, however, as shown in the uninfected plants from plots not treated with oxamyl, would be a downward trend (Gunasena, 1969) irrespective of the fact that the nutrient concentrations were established in whole plant dry matter at 56-61 DAP and from fourth leaf dry matter at 98-107 DAP. The increase in nutrient concentrations within plants infected by PCN would, therefore, contradict the normal nutrient uptake and accumulation patterns. This may suggest that PCN are influencing not only the nutrient uptake but also the pattern of uptake.

In the rate of foliar N experiment, in plots which had received only foliar water, the plants from oxamyl untreated plots contained a significantly lower concentration of N than plants from oxamyl treated plots. The application of foliar N to oxamyl untreated plots further raised the N concentration, to a significantly higher level than in the plants which had received only foliar water. The application of foliar N had, therefore, effectively increased the N concentration of PCN infected plants and had successfully by-passed the PCN damaged root system.

In the basal, tuber initiation and foliar N experiment, plant N concentrations were again successfully elevated by supplementary foliar N applications, except where all of the basal N was applied at planting. Where all of the basal N was applied at planting, however, plant N concentrations were similar to those of the Std (control) plants receiving the basal N split 50/50 between planting and tuber initiation. This reduction in N concentration may have been due to a loss of the available nitrogen as there is a large potential for high N leaching losses on this light free draining and well irrigated soil (Gunasena, 1969; Gunasena & Harris, 1971). As there was a corresponding reduction in the plant P concentration in the same treatment, it is possible that poor N uptake subsequently reduced P uptake, arising from the synergistic interaction of these nutrients (Lewis, 1986). It could be suggested that the effects of this treatment, giving nutrient concentrations closer to those in plants from oxamyl treated plots, were more in line with the expected nutrient concentrations, and should therefore have benefited the plant. This does not, however, appear to be the case, as the tuber yield from this treatment was lower than in the Std (control).

4.8 Conclusions

The pre-emergence and early post-emergence nutrition of the crop appears to be significantly affected by PCN infection. The results suggest that early nutrition of the plant has a marked effect on overall plant growth and yield, as greater early ground cover is essential for good final yield (Allen and Scott, 1992). The experimental foliar treatments demonstrated no significant benefits to the growth or yield of the crop. However, a yield improvement on average of 4.0 t/ha (16%) above the non-nematicide control, from the addition of a 4% supplementary foliar N, 1.7% P foliar application followed by four 4% foliar N applications or the addition of a 3.4% P foliar application with a five 4% foliar N programme, is considerable and worthy of further investigation. There is no evidence to suggest that a five foliar nitrogen spray programme is more beneficial to crop growth and yield than a four spray foliar nitrogen programme. It has also been shown that it is necessary, even with experiments within the same experimental area, to maintain both nematicide and non-nematicide control treatments. These are required to quantify yield changes relative to a non-infected crop and as tolerance improvements or reductions in relation to a base tolerance level. The application of foliar phosphate at greater than 1.7% concentration requires the addition of urea if scorch and loss of green leaf area are to be prevented. All yield increases were associated with increases in the number of tubers. Increasing rates of foliar N did show evidence of linear correlation with ground cover at 76 DAP and this may mean that early applications of N at a higher rate may be beneficial. The results also suggested that split applications of 120 kg N/ha at planting and 120 kg N/ha at tuber initiation were necessary for the season-long nutrition of the PCN infected plants. The higher rates of N at planting, 180 and 240 kg N/ha, however, caused significant loss of ground cover in the latter part of the season, gave similar or reduced yields to those seen in the non-nematicide control and were not beneficial to early growth. The yield benefits from foliar N and foliar P were not solely from benefits to ground cover and may have been caused by better root development and increased root nutrient uptake. Leaf discolouration was less where foliar P had been applied and, taken in conjunction with dark-green leaf appearance and chlorophyll readings, P may be a limiting nutrient in the PCN infected plants within these experiments. However, as increasing the P nutrition of the plant by soil application of granular fertilisers, during the early stages of plant development, has been shown to be ineffective, earlier foliar applications may be the only alternative. Root invasion may be a more suitable variate than Pi on which to base covariance analysis in experiments that include nematicide treatments. Further work is needed to encompass a wider range of invasions in one experiment and from which the true relationships between PCN invasion, nutrient uptake and yield can be seen.

5. Field and glasshouse experiments, 1998

5.1 Introduction

The research carried out in the 1996 experiments showed no real tolerance benefits from applications of broadcast granular or liquid placed fertiliser. The experiment with individual or combined applications of foliar N, P and K, however, showed that applications of foliar P, foliar N and Foliar N + K could benefit percentage ground cover, leaf area index, tuber yield and consequently the tolerance of PCN infected plants. In the 1997 experiments, the application regime of seedbed N and the use of supplementary foliar N and foliar P was developed to further investigate fertiliser effects on the potato plant's tolerance of PCN invasion. These 1997 experiments demonstrated, for a second year, small tolerance benefits from a programme of five 4% foliar N applications but also highlighted benefits to tuber yield from single early applications of foliar P within either a four or five application foliar N programme. However, the 1996 and 1997 experiments both highlighted a delay in plant emergence, slow post-emergent plant growth and lower percentage ground cover when the plants were infected with PCN. This poor early growth may well have been the result of reduced nutrient uptake by the PCN damaged roots which, when not infected, supply nutrients which increase the speed of plant emergence and the number of stems produced (Moorby, 1968; Moorby & Milthorpe, 1975). In addition, the small early ground cover would have reduced tuber yields because greater yields need large ground cover during early plant growth (Allen & Scott, 1992). Foliar nutrients applied during or after tuber initiation, therefore, could at best ameliorate nutrient deficiencies and stimulate later season plant growth, but could not remedy the yield limitation imposed by small early season ground cover. The 1997 experiments, also highlighted significant early season (56 to 58 DAP) reductions of N, P and K concentrations in plants infected by PCN. The 1998 experiments were, therefore, designed to investigate the nutrient status, in particular P status, of the PCN-infected pre-emergent and early post-emergent plant. The selection of P as opposed to N and K was based on the known influence of P on root growth and early canopy development (Mengel & Kirkby, 1987). The experiments were carried out in both field and glasshouse environments to investigate fertiliser and PCN environmental interactions. Trudgill (1980) had applied twice the standard rate of P, at planting, in both 'pot' and field experiments and reported significant increases in plant weight in the 'pot' experiments but no similar plant weight increases in field experiments. With this background of conflicting results, the 1998 experiments were designed to mimic the field experiment, as closely as possible, and allow comparisons to be made between the glasshouse and field based experiments with PCN and fertilisers. The experiment design included supplementary P in both broadcast granular and foliar applications to investigate whether either could increase the concentration of P within the plant, supplementing the early post-emergent P nutrition of the plants and, therefore, increase plant growth. Foliar applications were initiated when the plant ground cover attained 20%, which, although a small leaf target, was adequate for spray interception when used in conjunction with the band-spraying technique (BCPC, 1986). Foliar P was applied in a four spray sequence over a short time period to reduce the potential for foliage scorch. A cultivar of intermediate tolerance, Estima (Whitehead *et al.*, 1987), was chosen for this experiment so that the effects of PCN invasion would be reasonably obvious whilst also producing a reasonable yield.

5.1.1 Aims of the 1998 investigations

The hypothesis tested was that: 'Increasing the supply of fertiliser phosphate, either as broadcast granular or foliar P, will prevent the pre-tuber initiation reduction in P concentration in PCN-infected plants and enhance early plant growth, ground cover and final yields, to levels similar to those found in plants not infected by PCN'.

Field and glasshouse experiments investigated whether :

1) the nutrient status of the field grown potato plant is affected by PCN invasion at 7-10 days after plant emergence and, the field and glasshouse grown potato plant at 7-10 days after the start of tuber initiation.

2) an increase in P application rate at planting time can increase the P status of the PCN infected plant and thereby increase the rate of early plant growth.

3) pre tuber initiation applications of foliar P can increase the nutrient status of the PCN infected plant and thereby increase the rate of early plant growth.

The title for the field experiment is :

The growth and yield responses of field grown potatoes to supplementary broadcast granular or foliar applied P when infected by potato cyst nematodes.

The title for the glasshouse experiment is:

The growth response of glasshouse grown potatoes to supplementary broadcast granular or foliar applied P when infected by potato cyst nematodes.

5.2 General material and methods

The field experiment site, at Harper Adams University College, Newport, Shropshire, UK, grid reference SJ 705194 (O.S., 1987) was a Bridgnorth series slightly stoney sandy loam (Beard, 1988) with ADAS (Anon, 1994) nutrient indices of : N = 0; P = 5 (94 mg P/l); K = 5 (708 mg K/l); Mg = 3 (132 mg Mg/l) and pH 7.9. All plots were three beds (six rows) wide and 8m long, with each bed split into two rows 91.5 cm wide at planting. Each plot consisted of a central two rows, used for non-destructive analysis and final yield, a row at either side of the central rows, for destructive plant analysis and two outer guard rows. Primary cultivations: ploughed to 30 cm depth and bed-forming two days prior to planting, followed by bed-tilling, bed re-forming and stone separation on the day of planting. Chitted potato seed *(Solanum* *tuberosum*) cv. Estima (super elite grade 1, graded at 55mm) was planted on 29th April at 15-20 cm depth and 28-30 cm spacing (approximately 39,000 seed tubers/ha) using a tractor mounted Faun automatic potato planter. Seedbed granular fertilisers and nematicides were broadcast by hand onto formed beds on the day of planting, prior to bed-tilling; nematicide treated plots received oxamyl as Vydate (10% oxamyl w/w, gr., Du Pont (UK)) at 5.5 kg a.i./ha; N was applied at 110 kg N/ha as ammonium nitrate (Hydro ExtraN, 34.5% N); phosphates were applied, as required by the treatments, as triple super phosphate (43% P_2O_5 soluble in water); potassium applications were not required at soil index 5 (Anon, 1994). Tuber initiation nitrogen as ammonium nitrate (Hydro ExtraN, 34.5% N) was broadcast during tuber initiation, 42 DAP, at a rate of 138 kg N/ha. Foliar applications were made with an Azo, two metre, CO_2 powered plot sprayer, delivering 300 litres/ha at 200 Kpa, with Lurmark 02E80 even spray nozzles. Foliar phosphate was supplied as ortho-phosphoric acid (54% P_2O_5, Hydro Agri (UK)). Treatments applied (Table 5.1) were as follows; 1, seedbed P at 100 kg P_2O_5/ha plus four sequential foliar applications of water, nematicide as Vydate at 5.5 kg a.i./ha; 2, seedbed P at 100 kg P_2O_5/ha plus four sequential foliar applications of water; 3, seedbed P at 110.2 kg P_2O_5/ha plus four sequential foliar applications of water; 4, seedbed P at 120.4 kg P_2O_5/ha plus four sequential foliar applications of water; 5, seedbed P at 100 kg P_2O_5/ha plus four sequential foliar applications of 0.85% P; 6, seedbed P at 100 kg P_2O_5/ha plus four sequential foliar applications of 1.7% P. The PCN population was identified as predominantly *G. rostochiensis* but with *G. pallida* also present at a very low level.

5.2.1 Specific to the field experiment

Four foliar P applications began at 36 DAP with an average of 5-day intervals between applications (Table 5.1). Treatments requiring no foliar P applications received foliar water applications on the same application timings. Experimental design was a randomised complete block with five replicates. Soil moisture deficits were maintained at a maximum of 35 mm by rain gun irrigation and were monitored using an Institute of Hydrology neutron probe moisture meter. Air and soil temperature, rainfall and irrigation were monitored throughout the season as listed in section 2.1. The crop was grown using standard agrochemical practices for a commercially grown potato crop, for the control of weeds and the disease 'late blight'. The mean initial PCN population density, identified as predominantly *G. rostochiensis* with a trace of *G. pallida*, was 33 eggs/g soil.

Table 5.1. Fertiliser nutrients applied in field and glasshouse investigations of the response to pre-emergent and early post emergent P of potatoes infected by potato cyst nematodes.

treatment code [a]	P applications (kg P_2O_5/ha): broadcast at planting	P applications (kg P_2O_5/ha): foliar applications Field 36, 42, 46, 51 [b] Glass 27, 33, 37, 42 [c]	total P_2O_5 applied	nematicide used
Std +O	100	water only	100	oxamyl
Std	100	water only	100	none
Std + BP1	110	water only	110.2	none
Std + BP2	120	water only	120.4	none
Std + FP1	100	2.55, 2.55, 2.55, 2.55	110.2	none
Std + FP2	100	5.1, 5.1, 5.1, 5.1	120.4	none

[a] Std = standard fertiliser practice, + O = plus oxamyl, + BP1 = broadcast granular triple superphosphate at 10 Kg P_2O_5/ha, + BP2 = broadcast granular triple superphosphate at 20 Kg P_2O_5/ha, + FP1 = plus four applications of foliar P at 2.55 kg P_2O_5/ha per application, +FP2 = plus four applications of foliar P at 5.1 kg P_2O_5/ha per application.
[b] days after planting of field experiment
[c] days after planting of glasshouse experiment.

5.2.2 Specific to the glasshouse experiment

Four foliar P applications began at 27 DAP with an average of 5-day intervals between applications (Table 5.1). Treatments with no foliar P received foliar water applications at the same application timings. Experimental design was a randomised complete block with eight replicates. Pots for use in the glasshouse were filled with soil taken from the field experiment, after the incorporation of the nematicide and granular fertilisers, following the plot order. Each pot was 30cm diameter, was sampled for PCN infestation and planted with an Estima potato tuber at 20cm depth on the same day as the field experiment was planted, and formed one replicate. No additional lighting was used in the glasshouse, water was supplied from above as required, soil temperature was monitored using a soil temperature thermometer and air temperature monitored with a Tinytag® datalogger. Tuber initiation nitrogen as ammonium nitrate (Hydro ExtraN, 34.5% N) was applied during tuber initiation, 43 DAP, at a rate of 138 kg N/ha. The experiment was terminated at 47 DAP, when the plant tops were removed at soil level, split into component parts, weighed, leaves measured for LAI with a Delta T leaf area meter, and all components were oven dried and reweighed. The plant roots and lower stems were gently removed from the pots. The roots were then washed, a 2g subsample was taken and stored in FAA for subsequent root invasion analysis. The stems and remaining roots were then weighed, dried and re-weighed. Final PCN population density samples were taken from the soil after removal of the roots and stems, and dried in a heated and ventilated drying room. The mean initial PCN population density, identified as *G. rostochiensis* with a trace of *G. pallida*, was 34 eggs/g soil.

5.3 Results of the field experiment

The growth and yield responses of field grown potatoes to supplementary broadcast granular or foliar applied P when infected by potato cyst nematodes.

5.3.1 PCN populations

The PCN populations within the experimental area were identified by isoelectric focusing as predominantly *G. rostochiensis* but a faint band also suggested the presence of some *G. pallida*.

Table 5.2. Initial (Pi) and final (Pf) PCN population densities (eggs/g soil), Pf/Pi ratios and potato root invasion by PCN (juveniles/g root) at 30 & 57 days after planting (DAP) in a field investigation of the growth and yield response to supplementary broadcast granular and foliar P of potatoes infected by potato cyst nematodes.

treatment	Pi (eggs/g soil)	Pf (eggs/g soil)	Pf/Pi	root invasion (juveniles/g root) 30 DAP	57 DAP
Std + O [a]	35	124	4.0	190	220
Std	45	489	11.8	1520	870
Std + BP1	29	425	16.5	1890	1050
Std + BP2	33	473	14.5	1400	920
Std + FP1	29	438	19.9	1530	1040
Std + FP2	29	416	19.9	1600	910
mean	33	394	14.4	1355	835
overall SED	6.8	83.7	5.27	277.8	147.0
d.f.	20	20	20	20	20
CV%	32.3	33.6	57.6	32.4	27.8
<u>Significance ($P =$)</u>					
overall	n.s.	0.003	n.s.	<0.001	<0.001
oxamyl vs no oxamyl	n.s.	<0.001	0.006	<0.001	<0.001
std vs std + BP & FP	0.011	n.s.	n.s.	n.s.	n.s.
+ BP vs + FP	n.s.	n.s.	n.s.	n.s.	n.s.
P1 vs P2	n.s.	n.s.	n.s.	n.s.	n.s.
+BP vs +FP* P1 vs P2	n.s.	n.s.	n.s.	n.s.	n.s.

[a] see table 5.1.

i) Initial population density

The initial PCN population densities, Pi, (eggs/g soil) did not differ significantly between the experimental treatments (Table 5.2). The range of mean treatment Pi's was relatively small, 29 to 35 eggs/g soil, except for the plots of the standard treatment (Std) where the mean was

45 eggs/g soil. The CV of 32.3% suggests that population densities of PCN were quite variable between plots.

ii) Final population density

The final PCN population densities (mean of 394 eggs/g soil) were significantly (P <0.001) lower where plots had been treated with oxamyl at planting. There were no significant effects from the supplementary P applications (Table 5.2).

iii) Pf/Pi ratios

The Pf/Pi ratios were significantly (P = 0.006) lower where plots had been treated with oxamyl at planting (Table 5.2). Applying supplementary P did not affect the Pf/Pi ratios.

iv) Potato root invasion by PCN

a) 30 DAP

The number of PCN juveniles, all stages, counted in the stained potato roots at 30 DAP were significantly (P<0.001) reduced by the pre-planting application of oxamyl to the plots (Table 5.2). There were no significant differences arising from the application of higher rates of broadcast granular phosphate and no differences found in the roots of plants from plots allocated for foliar P application (foliar application began at 36 DAP).

b) 57 DAP

The application of oxamyl to plots significantly (P<0.001) reduced the number of PCN juveniles found in potato roots. There were no significant differences attributable to the application of additional phosphate either as broadcast or foliar applications (Table 5.2).

Table 5.3. The percentage emergence of potato plants in an investigation of the growth and yield response to supplementary broadcast granular and foliar of potatoes infected by potato cyst nematodes.

treatment	days after planting 19	22	25	27	29	33
Std + O [a]	9.0	24.8	48.6	63.7	82.7	100
Std	7.4	20.9	42.8	62.6	82.7	100
Std + BP1	7.1	18.6	40.9	61.7	85.0	100
Std + BP2	7.3	21.1	42.1	56.0	73.4	100
Std + FP1	4.1	16.5	38.8	55.5	79.1	100
Std + FP2	2.8	14.2	36.0	62.6	89.0	100
mean	6.3	19.4	41.5	60.4	82.0	100
SED	3.75	4.39	5.09	5.34	5.04	n.a. [b]
d.f.	20	20	20	20	20	n.a.
CV%	94.3	35.9	19.4	14.0	9.7	n.a.
<u>Significance (*P* =)</u>						
overall	n.s.	n.s.	n.s.	n.s.	n.s.	n.a.
oxamyl vs no oxamyl	n.s.	n.s.	0.044	n.s.	n.s.	n.a.
std vs std + BP & FP	n.s	n.s.	n.s.	n.s.	n.s.	n.a.
+ BP vs + FP	n.s.	n.s.	n.s.	n.s.	n.s.	n.a.
P1 vs P2	n.s.	n.s.	n.s.	n.s.	n.s.	n.a.
+BP vs +FP* P1 vs P2	n.s.	n.s.	n.s.	n.s.	n.s.	n.a.

[a] see table 5.1.

[b] analysis not applicable.

5.3.2 Plant growth

i) Plant emergence

Plant emergence, estimated at 19, 22, 25, 27, 29 and 33 DAP was not significantly affected by increased applications of broadcast granular phosphate. Oxamyl application to plots significantly increased the plant emergence recorded at 25 DAP (Table 5.3).

ii) Plant fresh-weight at 30 DAP

There was weak evidence that the application of oxamyl to plots significantly ($P = 0.052$) improved the total plant fresh-weight at 30 DAP (Table 5.4). There were no differences between the fresh-weights of plants arising from the application of increased quantities of broadcast granular phosphate. Foliar P applications were not initiated until six days after this assessment.

iii) Plant fresh-weight at 57 DAP

Plants in oxamyl treated plots had significantly ($P = 0.035$) higher above ground fresh-weights and very significantly ($P<0.001$) smaller root fresh-weight compared to plants in plots not treated with oxamyl (Table 5.4). There was some evidence that the total fresh-weights of plants were greater in oxamyl treated plots ($P = 0.053$). In plots not treated with oxamyl, root fresh-weight was significantly ($P = 0.002$) lower where additional broadcast granular P was applied at 20.4 kg P_2O_5/ha than where plants received foliar P at 10.2 kg P_2O_5/ha. The supplementary P applications of 20.4 kg P_2O_5/ha, either as broadcast granular or foliar applications, produced similar tuber fresh-weights to those of plants from oxamyl treated plots, and greater than plants where the standard or smaller quantity of P was applied, however, these were not significant differences (Table 5.4).

iv) Leaf area at 57 DAP

There were no significant differences in leaf area (cm^2) from any treatment applications. The greatest leaf area (10950 cm^2) was seen in plants from oxamyl treated plots and the smallest

(8861 cm²) was in plants receiving foliar P at 20.4 kg P_2O_5/ha, The application of supplementary P did not increase leaf area (Table 5.4).

Table 5.4. Potato plant fresh-weight (g) at 30 and 57 days after planting (DAP) and leaf area (cm²) at 57 DAP in a field investigation of the growth and yield response to supplementary broadcast granular and foliar P of potatoes infected by potato cyst nematodes.

	30 DAP	57 DAP				
treatment	total fwt	total fwt	upper [a] fwt	roots fwt	tuber fwt	leaf area (cm²)
Std + O [b]	283.8	890	679	9.47	146.3	10950
Std	251.8	807	619	15.25	120.9	10253
Std + BP1	241.0	729	560	14.09	111.0	9394
Std + BP2	241.7	754	544	13.46	149.3	9436
Std + FP1	239.6	794	621	16.37	101.2	10250
Std + FP2	225.0	742	543	13.85	141.0	8861
mean	247.1	786	594	13.75	128.3	9857
SED	27.57	78.4	58.1	1.418	28.40	912.3
d.f.	20	20	20	20	20	20
CV%	17.6	15.8	15.5	16.3	35.0	14.6
<u>Significance (P =)</u>						
overall	n.s.	n.s.	n.s.	0.002	n.s.	n.s.
oxamyl vs no oxamyl	0.052	0.053	0.035	<0.001	n.s.	n.s.
std vs std + BP & FP	n.s.	n.s	n.s.	n.s.	n.s.	n.s.
+ BP vs + FP	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
P1 vs P2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
+BP vs +FP* P1 vs P2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

[a] upper = all above ground plant parts.

[b] see Table 5.1.

Table 5.5. Nutrient concentrations of whole plant dry matter at 30 and 57 DAP in an investigation of the growth and yield response to supplementary broadcast granular and foliar P of potatoes infected by potato cyst nematodes.

	30 DAP			57 DAP		
treatment	%N	%P	%K	%N	%P	%K
Std + O [a]	4.82	0.687	8.38	3.70	0.543	7.46
Std	4.69	0.673	7.96	3.71	0.509	7.09
Std + BP1	4.68	0.674	7.49	3.73	0.490	6.67
Std + BP2	4.64	0.663	7.76	3.59	0.495	7.11
Std + FP1	4.56	0.673	7.74	3.72	0.523	7.73
Std + FP2	4.59	0.661	7.52	3.44	0.498	6.73
mean	4.66	0.672	7.81	3.65	0.510	7.13
SED	0.111	0.0197	0.286	0.273	0.0323	0.401
d.f.	20	20	20	20	20	n.s.
CV%	3.8	4.6	5.8	11.8	10.0	8.9
<u>Significance (*P* =)</u>						
overall	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
oxamyl vs no oxamyl	0.043	n.s.	0.006	n.s.	n.s.	n.s.
std vs std + BP & FP	n.s	n.s.	n.s.	n.s.	n.s.	n.s.
+ BP vs + FP	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
P1 vs P2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
+BP vs +FP*P1 vs P2	n.s.	n.s.	n.s.	n.s.	n.s.	0.019.

[a] see table 5.1.

5.3.3 Nutrient status

i) Whole plant at 30 DAP

Plants from oxamyl treated plots contained significantly higher concentrations of N ($P = 0.043$) and K ($P = 0.006$) than plants from oxamyl untreated plots, but there were no differences in

P concentration (Table 5.5). Applying supplementary granular P did not increase the N, P or K concentration within plants from oxamyl untreated plots. No foliar P applications had been made at this assessment time.

ii) Whole plant at 57 DAP

No significant differences in N, P or K concentration arose from the application of oxamyl to plots and concentrations of N and P were not affected by applications of increased quantities of P. However, significant ($P = 0.019$) effects on the K concentration were found when low and high applications of P, either broadcast or foliar applied were compared: the K concentration was higher where the higher quantity of broadcast granular (7.11% K) or the lower quantity of foliar P (7.73% K) was applied (Table 5.5).

5.3.4 Tuber yield at 118 DAP

Tuber yields were significantly ($P<0.001$) greater in oxamyl treated plots, in the 60 to 80 mm grade, ware grade and total tuber yield (Table 5.6). In plots not treated with oxamyl, the application of foliar P at 20.4 kg P_2O_5/ha significantly reduced the yield in the 60-80 mm grade compared to the Std treatment. No application of supplementary P improved the tuber yield beyond that seen in plots receiving the Std P application (Table 5.6).

i) Tolerance to PCN

The tolerance of the plants to PCN infection, expressed as a percentage of the yield produced by plants in plots treated with oxamyl, showed the yields in all oxamyl untreated plots were significantly ($P<0.001$) lower than the oxamyl treated yield. The application of increased quantities of P reduced the tolerance ratios, though not significantly, compared to the Std P application (Table 5.6).

Table 5.6. Potato tuber yield (t/ha) at harvest (118 DAP) and tolerance ratio in an investigation of the growth and yield response to supplementary broadcast granular and foliar P of potatoes infected by potato cyst nematodes.

treatment	size grade (mm) <40	40-60	60-80	ware	total	tolerance ratio % [a]
Std + O [b]	4.46	30.9	23.3	54.2	58.7	100
Std	4.66	29.8	16.1	46.0	50.6	86.3
Std + BP1	4.65	28.9	13.6	42.5	47.1	80.3
Std + BP2	4.69	28.4	15.3	43.7	48.4	82.5
Std + FP1	4.67	29.1	15.5	44.6	49.3	84.0
Std + FP2	4.58	27.6	13.0	40.5	45.1	76.9
mean	4.62	29.1	16.1	45.3	49.9	85
SED	0.869	2.15	2.70	2.89	3.24	5.52
d.f.	20	20	20	20	20	n.s.
CV%	29.8	11.7	26.5	10.1	10.3	10.3
<u>Significance (P =)</u>						
overall	n.s.	n.s.	0.015	0.003	0.009	0.009
oxamyl vs no oxamyl	n.s.	n.s.	<0.001	<0.001	<0.001	<0.001
std vs std + BP & FP	n.s	n.s.	n.s.	n.s.	n.s.	n.s.
+ BP vs + FP	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
P1 vs P2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
+BP vs +FP * P1 vs P2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

[a] tolerance ratio calculated as percentage yield of oxamyl treated yield.

[b] see table 5.1.

ii) Effect of covariance of yields

Total tuber yield was subjected to covariance analysis to remove the underlying differences of initial PCN population densities and root invasion between the plots, at 30 and 57 DAP. The yields in oxamyl treated plots remained significantly ($P<0.001$) greater than those in oxamyl untreated plots when the Pi was used as the covariate (Table 5.7). Using root invasion at 30 DAP as the covariate removed the significant differences seen in the Anova without covariance, and the highest yields were in plots receiving the Std P (52.3 t/ha) and broadcast granular P applications at 20.4 kg P_2O_5/ha (52.4 t/ha). Using root invasion at 57 DAP as the covariate showed only significantly ($P = 0.038$) greater yields in oxamyl treated plots than those in plots which had received supplementary P (Table 5.7). The use of covariance analysis does, therefore, make a difference to the significance that can be attached to differences in the final yields and, consequently, to the interpretation of treatments effects.

iii) PCN relationship to total crop yield

a) Simple linear regression

No significant relationship was found between Pi and total tuber yield, so no r^2 values could be derived from the data. There were very significant ($P<0.001$) relationships of root invasion and $\log_e$ root invasion at 30 DAP with total yield, but r^2 values suggested that the untransformed root invasion gave a much better ($r^2 = 0.71$) explanation of the variance than did the $\log_e$ root invasion ($r^2 = 0.52$) (Figure 5.1 and 5.2). Root invasion and $\log_e$ root invasion measured at 57 DAP were also significantly ($P = 0.004$ & $P = 0.002$, respectively) related to final yield but the relationship was less well explained ($r^2 = 0.23$ & $r^2 = 0.28$, respectively) than at 30 DAP. The most suitable data for use as covariates are probably the untransformed root invasion counts at 30 DAP.

Table 5.7. Effect of covariance on the analysis of total tuber yields (t/ha) in an investigation of the growth and yield responses to supplementary broadcast granular and foliar P of potatoes infected by potato cyst nematodes.

	covariance type			
treatment	none	Pi [a]	invasion1 [b]	invasion2 [c]
Std + O [a]	58.7	59.0	47.1	58.1
Std	50.6	52.5	52.3	50.7
Std + BP1	47.1	46.4	52.4	47.3
Std + BP2	48.4	48.4	48.9	48.5
Std + FP1	49.3	48.5	51.0	49.5
Std + FP2	45.1	44.4	47.5	45.2
mean	49.9	49.9	49.9	49.9
SED	3.24	3.26	2.13	3.99
d.f.	20	20	20	20
CV%	10.3	9.9	5.6	10.5
<u>Significance (P =)</u>				
covariance	n.a.	n.s.	<0.001	n.s.
overall	0.009	0.004	n.s.	0.038
oxamyl vs no oxamyl	<0.001	<0.001	n.s.	n.s.
std vs std + BP & FP	n.s.	n.s.	n.s.	n.s.
+ BP vs + FP	n.s.	n.s.	n.s.	n.s.
P1 vs P2	n.s.	n.s.	n.s.	n.s.
+BP vs +FP* P1 vs P2	n.s.	n.s.	n.s.	n.s.

[a] Initial PCN population density (eggs/g soil)
[b] PCN invasion of roots (juveniles/g root) 30 days after planting.
[c] PCN invasion of roots (juveniles/g root) 57 days after planting.
[d] see table 5.1.
[e] not applicable to analysis.

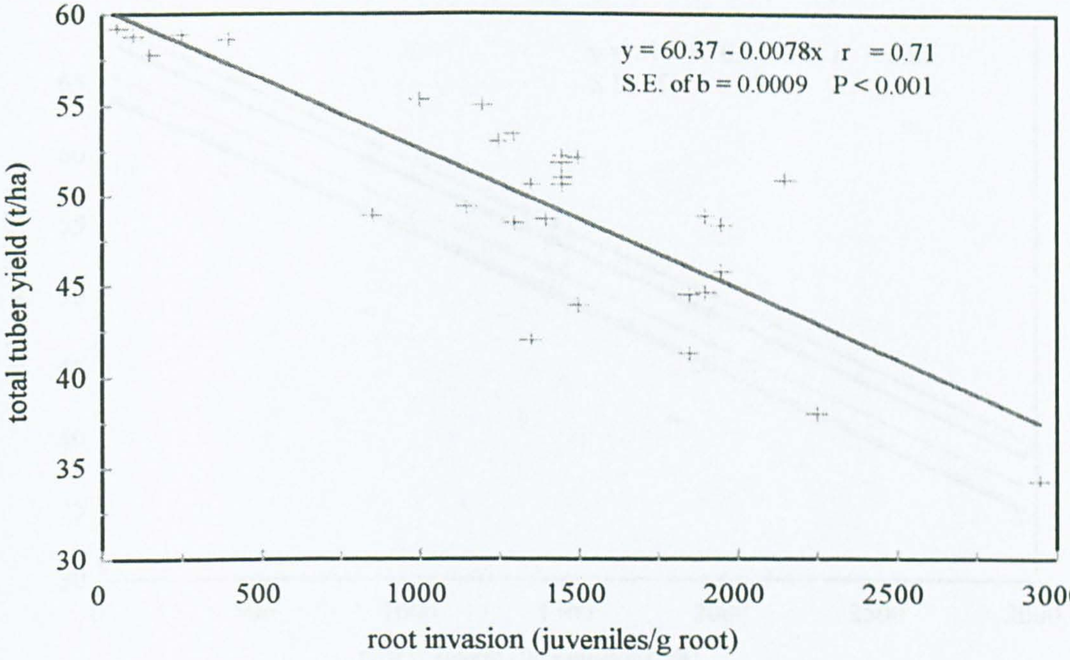

Figure 5.1. The simple linear relationship between PCN root invasion at 30 DAP and total tuber yield at harvest (118 DAP) in an investigation of the growth and yield responses to supplementary broadcast and foliar P of potatoes infected by potato cyst nematodes.

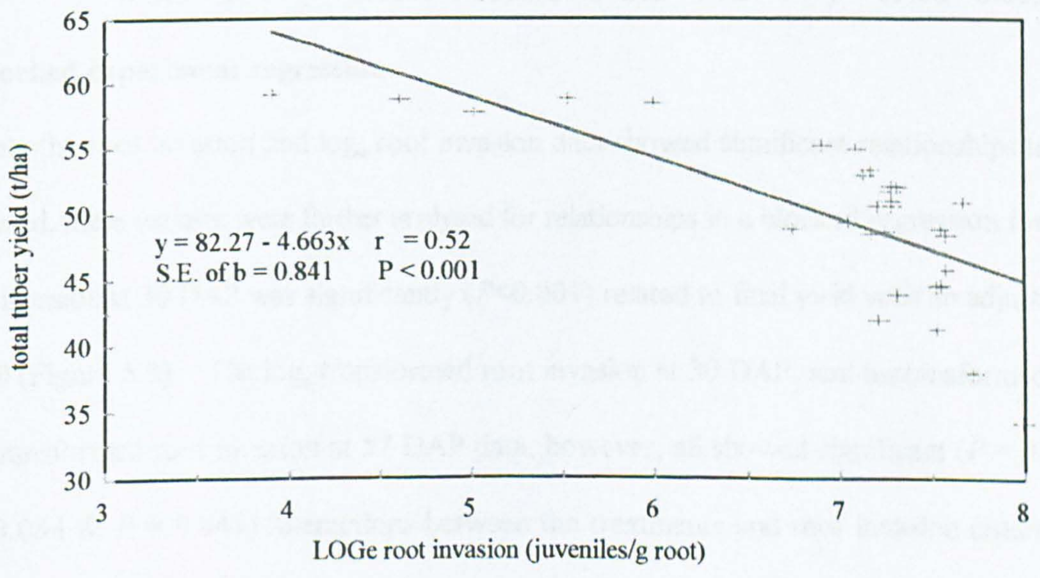

Figure 5.2. The simple linear relationship between $\log_e$ PCN root invasion at 30 DAP and total tuber yield at harvest (118 DAP) in an investigation of the growth and yield responses to supplementary broadcast and foliar P of potatoes infected by potato cyst nematodes.

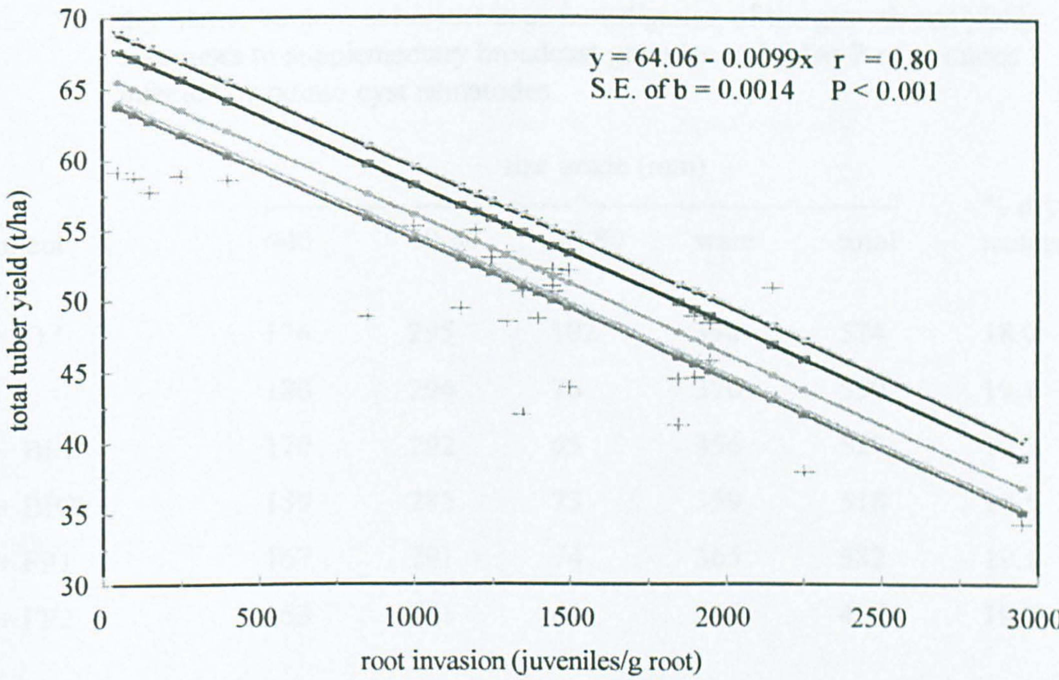

Figure 5.3. Linear relationship (blocked experiment) between PCN root invasion at 30 DAP and total tuber yield at harvest (118 DAP) in a field investigation of the growth and yield responses to supplementary broadcast granular and foliar P of potatoes infected by potato cyst nematodes.

[a] Regression line parameters :

■ Std + O	$y = 64.06 - 0.0099x$,	▼ Std (control)	$y = 58.93 - 0.0099x$
▲ Std + BP1	$y = 58.75 - 0.0099x$,	● Std + BP2	$y = 62.32 - 0.0099x$
⊠ Std + FP1	$y = 60.19 - 0.0099x$,	⧗ Std + FP2	$y = 63.68 - 0.0099x$

b) Blocked experiment regression

As only the root invasion and $\log_e$ root invasion data showed significant relationships to the final yield, these variates were further analysed for relationships in a blocked regression format. Root invasion at 30 DAP was significantly (P<0.001) related to final yield with an adjusted r^2 = 0.80 (Figure 5.3). The $\log_e$ transformed root invasion at 30 DAP, and untransformed and $\log_e$ transformed root invasion at 57 DAP data, however, all showed significant (P = 0.006, P = 0.034 & P = 0.043) interactions between the treatments and root invasion counts, so further analysis of the relationship would be invalid. It is suggested that only the data for root invasion counts at 30 DAP is suitable as a covariate for yield analysis of this blocked experiment and that a significant (P<0.001) relationship between root invasion counts at 30 DAP and yield has been shown.

Table 5.8. Graded numbers of potato tubers per plot at harvest (118 DAP) and the tuber dry matter content at harvest in an investigation of the growth and yield responses to supplementary broadcast granular and foliar P of potatoes infected by potato cyst nematodes.

treatment	size grade (mm) <40	40-60	60-80	ware	total	% dry matter
Std + O [a]	176	295	102	398	574	18.0
Std	180	294	76	370	550	19.1
Std + BP1	170	292	65	356	527	19.5
Std + BP2	159	285	73	359	518	19.5
Std + FP1	167	291	74	365	532	19.1
Std + FP2	153	281	63	344	497	19.7
mean	168	290	76	365	533	19.1
SED	27.9	27.7	11.1	26.2	50.2	0.50
d.f.	20	20	20	20	20	20
CV%	26.4	15.1	23.2	11.3	14.9	4.2
Significance (*P*=)						
overall	n.s.	n.s.	0.025	n.s.	n.s.	0.031
oxamyl vs no oxamyl	n.s.	n.s.	0.001	n.s.	n.s.	0.002
std vs std + BP & FP	n.s	n.s.	n.s.	n.s.	n.s.	n.s.
+ BP vs + FP	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
P1 vs P2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
+BP vs +FP* P1 vs P2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

[a] see table 5.1.

iv) Tuber number

There were significantly ($P = 0.001$) more tubers in the 60 to 80 mm grade in oxamyl treated plots. There were no significant differences from increased quantities of P as either broadcast granular or foliar applications. The standard application of P gave the greatest tuber numbers in all plots not treated with oxamyl (Table 5.8).

v) Tuber dry matter

Dry matter content of tubers was significantly ($P = 0.002$) lower in oxamyl treated plots than in tubers from oxamyl untreated plots. There were no significant effects on the tuber dry matter content from supplementary P application (Table 5.8).

5.4 Results of the glasshouse experiment

The growth response of glasshouse grown potatoes to supplementary broadcast granular or foliar applied phosphate when infected by potato cyst nematodes.

5.4.1 PCN populations

The PCN populations recorded within the experimental area were identified by isoelectric focusing as predominantly *G. rostochiensis* but a faint band also suggested the presence of some *G. pallida*.

i) Initial population density

The initial PCN population densities, Pi, (eggs/g soil) did not differ significantly between the experimental treatments (Table 5.9). The range of mean treatment Pi's was relatively narrow at 29 to 41 eggs/g soil, but the CV of 41.6% suggests the PCN populations were quite variable between plots.

ii) Potato root invasion by PCN

The number of PCN juveniles, all stages, counted in the stained potato roots at 47 DAP were not significantly affected by the application of oxamyl or supplementary P (Table 5.9). The greatest numbers of juveniles (1094 juveniles/g root) was counted in roots of plant's from plots receiving increased broadcast granular P at 10.2 kg P_2O_5/ha.

Table 5.9. Initial (Pi) PCN population densities (eggs/g soil) and root invasion counts (juveniles/g root) at 47 DAP in a glasshouse investigation of the growth response to supplementary broadcast granular and foliar P of potatoes infected by potato cyst nematodes.

treatment	Pi (eggs/g soil)	root invasion at 47 DAP (juveniles/g root)
Std + O [a]	34	844
Std	29	838
Std + BP1	30	1094
Std + BP2	33	800
Std + FP1	41	988
Std + FP2	39	955
mean	34	920
overall SED	7.2	190.8
d.f.	35	34
CV%	41.6	41.5
<u>Significance (P =)</u>		
overall	n.s.	n.s.
oxamyl vs no oxamyl	n.s.	n.s.
std vs std + BP & FP	n.s.	n.s.
+ BP vs + FP	n.s.	n.s.
P1 vs P2	n.s.	n.s.
+BP vs +FP* P1 vs P2	n.s.	n.s.

[a] see table 5.1.

5.4.2 Plant growth

i) Fresh-weight at 47 DAP

Plants from oxamyl treated plots had significantly greater total (P = 0.009) and above- ground (P = 0.004) fresh-weight than plants from oxamyl untreated plots (Table 5.10). In pots not treated with oxamyl, the standard P application gave significantly higher total ($P = 0.006$) and above ground ($P = 0.021$) plant fresh-weights than those measured for plants where supplementary P had been applied. There were no significant root or tuber fresh-weights differences from any treatment application (Table 5.10).

Table 5.10. Plant growth at 47 DAP in a glasshouse investigation of the growth response to supplementary broadcast granular and foliar P of potatoes infected by potato cyst nematodes.

treatment	fresh-weight (g) total	upper	roots	tuber	tuber number	leaf area (cm^2)
Std + O [a]	441.7	319.3	25.70	68.0	16	5249
Std	431.9	303.4	30.98	67.6	13	5084
Std + BP1	376.8	279.8	31.22	39.2	12	4417
Std + BP2	354.6	261.6	25.74	41.4	11	4441
Std + FP1	348.1	258.8	21.91	44.0	11	4601
Std + FP2	355.5	268.3	25.07	34.4	13	3860
mean	384.8	281.9	26.77	49.1	13	4608
overall SED	31.73	18.89	3.668	16.86	2.3	355.8
d.f.	34	34	34	34	34	34
CV%	16.5	13.4	27.4	68.7	37.2	15.4
<u>Significance ($P =$)</u>						
overall	0.013	0.014	n.s.	n.s.	n.s.	0.006
oxamyl vs no oxamyl	0.009	0.004	n.s.	n.s.	0.043	0.009
std vs std + BP & FP	0.006	0.021	n.s.	n.s.	n.s.	0.011
+ BP vs + FP	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
P1 vs P2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
+BP vs +FP* P1 vs P2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

[a] see table 5.1.

ii) Tuber number at 47 DAP

Oxamyl application significantly ($P = 0.043$) increased the numbers of tubers at 47 DAP. No differences in tuber numbers were attributable to supplementary P applications (Table 5.10).

iii) Leaf area at 47 DAP

Oxamyl application significantly ($P = 0.009$) increased the leaf area at 47 DAP. In plots not treated with oxamyl, the standard P application produced significantly ($P = 0.011$) greater leaf area than in any plants receiving supplementary P. Applying foliar P at 10.2 kg P_2O_5/ha produced significantly ($P = 0.006$) greater leaf area than applying it at 20.4 kg P_2O_5/ha (Table 5.10).

5.4.3 Nutrient status at 47 DAP

Oxamyl application did not significantly affect the N, P or K concentration measured in the whole plant dry matter at 47 DAP. Applying the standard quantity of P gave significantly ($P = 0.029$) lower N concentrations than when supplementary P was applied (Table 5.11). Applying supplementary P via the foliar route resulted in significantly ($P = 0.004$) greater P concentrations in plant dry matter than where supplementary P was applied as broadcast granules (Table 5.11). There were no significant K concentration differences, although supplementary broadcast P did give rise to greater K concentrations than where foliar P was applied. Increasing the P concentration to levels above those measured within plants from plots treated with oxamyl did not increase the fresh-weights of plants from plots not treated with oxamyl (Figure 5.4).

Table 5.11. Nutrient concentrations in whole plant dry matter at 47 DAP in a glasshouse investigation of the growth response to supplementary broadcast granular and foliar P of potatoes infected by potato cyst nematodes.

treatment	%N	%P	%K
Std + O [a]	3.44	0.530	7.28
Std	3.25	0.515	7.18
Std + BP1	3.65	0.523	7.29
Std + BP2	3.65	0.529	7.28
Std + FP1	3.57	0.553	7.07
Std + FP2	3.57	0.599	7.08
mean	3.52	0.541	7.20
overall SED	0.203	0.0231	0.251
d.f.	34	34	34
CV%	11.5	8.5	7.0
<u>Significance (*P* =)</u>			
overall	n.s.	0.010	n.s.
oxamyl vs no oxamyl	n.s.	n.s.	n.s.
std vs std + BP & FP	0.029	n.s.	n.s.
+ BP vs + FP	n.s.	0.004	n.s.
P1 vs P2	n.s.	n.s.	n.s.
+BP vs +FP* P1 vs P2	n.s.	n.s.	n.s.

[a] see table 5.1.

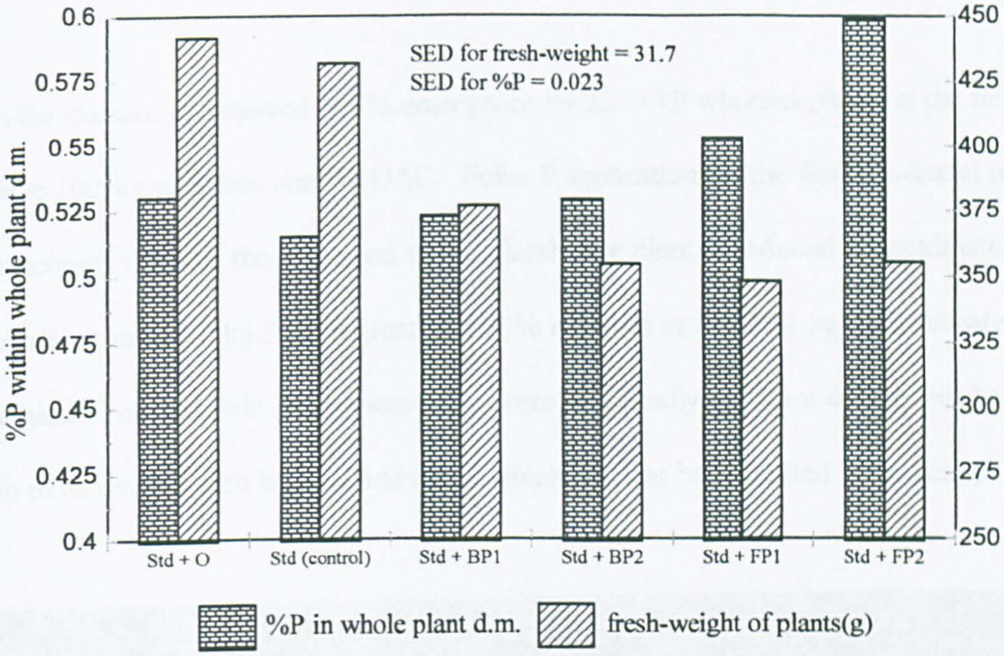

Figure 5.4 P concentrations and total plant fresh-weight at 47 DAP in an investigation of the plant growth response to supplementary broadcast granular and foliar P of potatoes infected by potato cyst nematodes.

5.5 General observations and environmental monitoring

In the field experiment, the application of fungicides for the control of late blight (*Phytophthora infestans*) and herbicides for weed control provided a disease and weed free environment for the experiment. Soil moisture deficits, measured with a neutron probe, were maintained at a mean of 10.6 mm for the season and reached a maximum of 34.2 mm at 71 DAP, when irrigation commenced. Soil temperatures, measured at tuber depth (15 to 20 cm) throughout the season, were a minimum of 8.4 °C, a maximum of 29.2 °C and a mean season temperature of 15.3 °C. The field experiment was terminated at 120 DAP, before the crop had naturally sensesced. In the glasshouse experiment, soil temperatures logged throughout the experiment period were a minimum of 15.5 °C, a maximum of 32.2 °C and an average of 19.5 °C. The air temperatures logged throughout the experiment period were a minimum of

7.7°C, a maximum of 36.5°C and an average of 19.2°C. The soil moisture was not measured for these plants but water was added on a daily basis to maintain a moist soil.

Plants in the glasshouse achieved 100% emergence by 22 DAP whereas plants in the field did not achieve 100% emergence until 33 DAP. Foliar P applications in the field produced no leaf damage (scorch) whereas those applied to the glasshouse plants produced approximately 5% leaf necrosis at the 10.2 kg P_2O_5/ha rate and 20% necrosis at the 20.4 kg P_2O_5/ha rate. In both the glasshouse and field experiment there were no visually apparent differences between plants in plots treated with oxamyl and those which had not been treated with oxamyl.

(left to right, foliar P 20.4 kg P_2O_5/ha, foliar P 10.2 kg P_2O_5/ha, foliar water)

Plate 5.1. Leaf damage caused by foliar P applications in an investigation of the plant growth response to supplementary broadcast granular and foliar P of potatoes infected by potato cyst nematodes.

5. 6 Discussion

The following discussions use the abbreviated treatment labels used in the tables of results. Similarly, the two standard treatments are defined as:

'Std (control)' this is the standard fertiliser practice with no other fertilisers applied and NO nematicide application, thus providing a base level of tuber yield and PCN tolerance from which treatment effects can be gauged.

'Std + O (control)' the standard fertiliser practice with no other fertilisers applied but WITH the nematicide oxamyl applied to the plots at planting, thus producing a yield as closely as possible to the yield expected in a PCN free soil.

5.6.1 PCN population studies

The initial population densities estimated for the field experiment plots and glasshouse pots ranged from 29 to 45 and 29 to 41 eggs/g soil, respectively, and did not differ significantly between treatment means in either experiment. Therefore, the field experiment area and the soil used in the glasshouse experiment was of a relatively uniform PCN infestation which also gave comparable PCN populations between the two experiments. Similar population densities of *G. pallida* have been shown by Whitehead *et al.* (1987) and Barker *et al.* (1998) to reduce the yield of Estima by 9.6% and 19.7%, respectively, and should, therefore, have provided an adequate level of infestation for these experiments.

The final PCN population densities were substantially increased in all field plots not treated with oxamyl, from a mean initial population density of 33 eggs/g soil to 448 eggs/g soil, and in the Std (control) plots to a mean of 489 eggs/g soil. Where plots were treated with oxamyl, however, the PCN population increased to only 124 eggs/g soil, which, although much reduced, would still be prohibitive for future potato crops without the use of control measures in addition to oxamyl application (Du Pont, 1996). The supplementary P applications did not substantially affect the final PCN population densities, which suggests that these nutrient applications had not influenced the suitability of the host plant for PCN development. Applications of P, however, can affect the final male/female ratio and the size obtained by female PCN (Raispere, 1990), and can cause significant reductions or increases in the population density (Trudgill, 1987), dependent on the quantity applied. No final population densities were measured in the glasshouse experiment (which was terminated at 47 DAP) as not enough time had passed for full PCN population development. Hammond-Cosak *et al.* (1990) suggest that females finally mature 40 days after the hatched juvenile enters the root, whilst Mulder & Van Der Wal (1997) indicate that, although mature females are found at six to seven weeks after plant emergence, fully developed eggs are not found until one month later. In either, event inadequate time would have elapsed. The reduction of PCN multiplication in plots treated with oxamyl was reflected in the Pf/Pi ratio of 4.0 as compared to 11.8 in the Std (control) plots. This increase in PCN population in the presence of a nematicide is not unusual as Whitehead *et al.* (1987a) report an identical Pf/Pi ratio of 4.0 where Estima was grown in soil treated with an equivalent rate of oxamyl at a similar infestation level of *G. pallida*. Whitehead *et al.* (1984) did, however, show that the use of oxamyl can achieve Pf/Pi ratios as low as 0.1 with some susceptible cultivars.

5.6.2 Root invasion

The type of root invasion analysis used in these experiments, i.e. using the whole root system, restricted analysis of the glasshouse experiment to just one at the termination of the experiment. It would have been possible to use some of the eight replicates for earlier analysis but this may have compromised subsequent plant analyses by increasing the CVs. Even with the eight-fold replication, the CVs reached values as high as 41.5%, which demonstrates both the inherent variability of the individual plant responses and the requirement for adequate replication.

In the field experiment the root invasion analysis at 30 and 57 DAP showed that only 190 and 220 juveniles/g root were present, respectively, in plants from oxamyl treated plots compared to the means of 1588 and 958 juveniles/g root in plants from plots not treated with oxamyl. This shows that the oxamyl application had significantly reduced PCN invasion and should, therefore, have provided an effectively PCN-free base from which to compare the growth and yield of PCN-infected plants. In contrast to this, the root invasion of the plants grown in the glasshouse, at 47 DAP, was the same in pots containing soil from oxamyl treated field plots as in pots containing oxamyl untreated soil. Whitehead *et al.* (1987a) have shown that oxamyl use in glasshouse pots effectively restricts PCN increase with susceptible cultivars and, therefore, a management or environment effect was likely. There were no differences between the soil used for the glasshouse and field experiments or the oxamyl incorporation itself as the soil for the glasshouse experiment was taken from the field experiment plots after the cultivations and oxamyl application had been made. There were, however, moisture and temperature differences between the two environments. As oxamyl is known to be weakly adsorbed and easily leached (Bromilow & Lord, 1979; Smelt & Leistra, 1992), the regular watering of the glasshouse plants may have led to a loss of oxamyl in the glasshouse experiment, thus allowing invasion to occur in oxamyl treated soil. In contrast to this, the field experiment received very little rainfall until 27 DAP and should, therefore, have given little opportunity for the oxamyl to be leached. Alternatively, the higher glasshouse soil moisture coupled with higher soil temperature, which averaged 22.2°C, may have contributed to accelerated oxamyl degradation, as shown by Suett (1994), and ineffective nematode control in the glasshouse. In contrast, the field soil temperatures averaged 12.0°C for the first 14 days and 15.1 °C up to 50 DAP, and this may represent the crucial difference between field and glasshouse experiments.

5.6.3 Plant emergence

The speed of plant emergence was significantly faster in plots treated with oxamyl (seen at 25 DAP) but was not affected by either oxamyl or supplementary P at any other time. These findings are similar to those from both the 1996 and 1997 experiments (section 3.6.2 and 4.7.3), except that plant emergence in plots not treated with oxamyl was retarded to a greater extent in the 1997 experiments. The PCN population densities were, however, much higher in the 1997 experiments and the potential for increased plant root damage and reductions of nutrient and water uptake would be accentuated in those circumstances. The emergence of plants in the glasshouse experiment was monitored but all plants emerged within three days of each other and no differences were found (results not shown).

5.6.4 Plant fresh-weight

i) Field experiment at 30 DAP

The plant analysis carried out in the field experiment at 30 DAP showed the total fresh-weight of plants was higher, though not significantly (P=0.052), from plots treated with oxamyl. This suggests that the greater number of juveniles found in the roots of plants from plots not treated with oxamyl had reduced plant growth even at this very early stage. In the UK, where the achievement of high potato crop yields requires high levels of incident radiation interception during the months of May to July (Allen & Scott, 1992) this loss of early growth will be detrimental to the final crop yield. One of the aims of the 1998 experiments was to investigate the potential for supplementary P application to encourage the early growth of plants infected with PCN. There were, however, no real benefits seen from the supplementary broadcast granular P applications. It is possible that the quantity of supplementary P may have been insufficient or, conversely, the supplementary application may not have increased the quantity of P available to the plant. The former explanation is unlikely as Trudgill (1980) applied 525 kg P_2O_5/ha and showed no benefit to leaf weights compared to those from field plots receiving 175 kg P_2O_5/ha, the standard quantity. Trudgill (1980) also showed that whilst the 525 kg P_2O_5/ha was three times the standard application, the available P in the soil increased by only 3%. These two arguments, however, are only relevant if the plant's requirement for P exceeded the supply at that time. This is unlikely, as the P concentrations were no different between plants lightly- and heavily-infected with PCN (section 5.3.3) and as the lightly-infected plants were growing well, they provided a suitable benchmark for comparison. Consequently, it is unlikely that P alone was limiting growth at that time. No applications of supplementary foliar P had been made by 30 DAP as plant emergence had achieved only 82% and virtually no crop cover existed to intercept foliar sprays.

ii) Field at 57 DAP and glasshouse at 47 DAP

The four spray supplementary foliar P programme was planned to commence as soon as possible after plant emergence. As the plants in the glasshouse experiment grew more rapidly than those in the field, the glasshouse foliar applications had to be started earlier to give similar plant spray interception characteristics and comparable plant P requirements. After the final foliar application, a further five days passed before leaf or plant sampling was carried out, which should have been sufficient for absorption of the foliar applied P as Lewis & Kettlewell (1993) have shown that the majority of P applied to leaves of the potato cultivar Estima is taken up between 24 and 96 hrs after application. Consequently, the glasshouse experiment was sampled and terminated at 47 DAP, 10 days earlier than the sampling time of field plots at 57 DAP. In the glasshouse experiment the total and upper plant fresh-weights were significantly (P = 0.009, P = 0.004) greater in plants from plots treated with oxamyl. Similarly, the Std (control) plants were significantly (P = 0.006, P = 0.021) heavier than all plants which had received supplementary P. These trends were also seen to some degree in the field experiment, where the total and upper fresh-weight of plants from plots treated with oxamyl were greater (P = 0.053, P = 0.035) than of plants from plots not treated with oxamyl. There was, however, no corresponding difference between the Std (control) and plants which had received supplementary P, and the weights of the Std (control) and low rate foliar P (Std + FP1) plants were almost equal. The greater fresh-weights of plants from oxamyl treated plots in the field are understandable in relation to the root invasion analysis, which showed these plants were subject to much lower PCN infection. The response in the glasshouse, however, is surprising, as plant roots from all of the treatments contained similar numbers of PCN juveniles. It is possible, therefore, that plants in oxamyl treated pots had derived some benefit from the oxamyl application, e.g. very early protection from invasion, before the speculated leaching or accelerated degradation of oxamyl had occurred (discussed in section 5.6.2). Of greater interest, however, is that the addition of supplementary P had caused plant fresh-weight reductions compared to the Std (control), in both the glasshouse and field experiment, with the exception of the Std + FP1 in the field. The results of the glasshouse experiment do not agree with the findings of Trudgill (1980), who showed that applying increased quantities of P to PCN-infected plants gave a significant leaf weight increase at seven weeks after planting and a two-fold haulm weight increase at 14 weeks after planting. The quantities of P applied by Trudgill (1980), however, were three times the standard quantity (525 v 175 kg P_2O_5/ha), whereas in these experiments a maximum of only 20% more than the standard recommended quantity of 100 kg P_2O_5/ha (Anon, 1994) was applied. In spite of this, the plant response in the field experiment is closer to Trudgill's (1980) field experiment, where the increased quantities of P had little effect on leaf weight at 11 weeks after planting. The field responses to the additional P were also similar to those found by De Ruijter (1998), who showed that applying 225 kg P/ha did not increase the total plant biomass (at 61 DAP) of plants infected with PCN beyond that seen in fumigated plots receiving no P fertilisers. The use of fumigants in fertiliser research, however, is debatable, as Whitehead (1978) suggests that these products can alter the availability of nutrients (e.g. N and P) which ultimately may distort the form of the plant response to any fertiliser treatments. In the absence of PCN, the normal plant response to fertiliser P applications is positive over a wide range of application quantities and soil types (Boyd & Dermott, 1964; Boyd & Dermott, 1967; Berryman *et al.*, 1973). Nevertheless, Boyd & Dermott (1967) and Berryman *et al.* (1973) report several experiments where additional P gave negative crop responses, and these were suggested to have arisen from interactions between N and P. Of particular relevance here, Boyd & Dermott (1967) reported that on the Newport and Bridgnorth series soils the negative response was accentuated by previous cropping, and they suggested that potatoes on these soil types within arable rotations should receive no more than 63 kg P_2O_5/ha to avoid this negative response. As the 1998 experiments were based on Bridgnorth series soil on an arable rotation, the supplementary P applications, which raised the application rate from 100 to 120 kg P_2O_5/ha, may have caused similar N and P interactions to those shown by Birch *et al.* (1967) and Boyd & Dermott (1967). In addition to this, Holliday (1963) shows that early plant growth can be adversely affected by P applications to soils with pH less than 6.0 and low soil P index or with pH greater than 6.0 and high soil P index.

In contrast to the total and upper plant fresh-weights, the root weights were significantly ($P < 0.001$) lower in the field experiment where plots had been treated with oxamyl. Although many experiments have shown that PCN infection produces less extensive and poorly distributed root systems (Evans *et al.*,1977; Haverkort *et al.*, 1994) the effects of PCN on root weight is quite varied. Fatemy & Evans (1986b) showed that heavily-infected root systems of the potato cultivar Désirée could be much larger than those of uninfected plants. In other work, root fresh-weights were reduced by PCN infection in three cultivars but increased in a fourth (Fatemy & Evans, 1986a). The reason for the differing responses is not clear but Fatemy & Evans (1986b) showed that PCN-infection reduces the ability of the roots to take up water, thus causing water stress within the plant which develops an increased ratio of roots to shoots because shoot growth is reduced relative to that of roots. This response reduces the production of above ground plant parts, thereby restricting water requirement and loss by transpiration whilst enhancing root growth and subsequently the water uptake potential of the plant. This explanation is all the more feasible because water stress is linked to the production of abscisic acid (ABA) which has been shown to limit shoot growth whilst stimulating root growth (Creelman *et al.*, 1990) and which has been reported by Fatemy *et al.* (1985) to be increased in plants infected by PCN. It is unlikely, however, that cultivar differences are the sole cause for the contrasting responses as Evans (1982a) and Fatemy & Evans (1986a) both used the cultivar Pentland Crown; in one report root weight was reduced but in the other it was increased. ABA has the function of a "wound hormone" and the increased ABA concentrations reported by Fatemy *et al.* (1985) could well be a wound signalling response which has the consequence of reducing the root to shoot ratio of PCN-infected plants.

The root weight trend highlighted in the field experiment was not duplicated in the glasshouse experiment where the root weights were very similar in all treatments. Where plants are grown in pots in the glasshouse, however, all of the root system can be easily collected. By contrast, collection of whole plant root systems from the field requires extensive excavation of plant samples which, in an experiment not specifically studying root growth, would be unwarranted. Nonetheless, Haverkort *et al.* (1994) showed that substantial root growth of PCN free roots occurs to depths of 100 cm. Therefore, by taking root samples in the field to only 30 cm, a significant proportion of roots may have been left behind in the oxamyl treated plots, leading to contrasting results between the field and glasshouse pots.

Applying supplementary P did not improve the root growth of PCN-infected plants in either the glasshouse or the field experiments. It could be expected that the plants from plots/pots receiving supplementary P would have produced larger root systems than the Std (control) as P is known to promote root growth (Mengel & Kirkby, 1987). The quantities of supplementary P may have been inadequate to elicit a response but, even where Trudgill (1980) applied 525 kg P_2O_5/ha no significant root weight increases were seen. In addition to this, Villagarcia & Franco (1984) showed that root growth of PCN infected potatoes was retarded when the strength of nutrient solution was increased from 120 to 240 ppm P_2O_5. These results, however, do highlight two important factors. Although applying additional quantities of P to the soil would be a logical step to overcome PCN-induced nutrient deficiencies, the nutrient analysis does not suggest that a deficiency existed (section 5.3.3). Therefore, no additional plant growth could be expected from supplementary applications. Further to this, the weight of the plant roots recovered would suggest that the root systems of heavily-infected plants was more extensive than those of the lightly-infected plants. Consequently, the efficiency of the heavily-infected root system must have been impaired, as demonstrated by Fatemy & Evans (1987b), and the ability of the roots to increase P uptake compromised. Within my experiments, however, foliar P applications offered a method of by-passing the damaged root system and a way to determine plant response to P applications which did not involve root uptake. As can be seen from the results, there were no upper-plant or root weight improvements arising from these applications. This must strengthen the argument that the availability of P was not the primary factor limiting plant growth. It is suggested, therefore, that a separate mechanism within the plant may be responsible for the lack of plant response to the supplementary P or indeed the response of plants to adequate supplies with P when infected by PCN. Van Oijen *et al* (1995) speculated that hormonal responses to PCN infection could be associated with a decreased allocation of biomass to shoots in favour of root growth. Melakeberhan & Webster (1993) add weight to this hypothesis by suggesting that phytohormone production in root tissues, and especially within root tips, could be disrupted by root damage from PCN infection. These suggestions are not purely speculative, as Evans (1982b) and Fatemy *et. al.* (1985) have shown that ABA concentrations were increased within plants infected with PCN. Furthermore, Fatemy *et al.* (1985) show that, although both root and shoot weights were reduced by PCN infection, the ratio of root to shoot was increased. This observation is frequent in PCN research and has been reported by many others (e.g. Evans, 1982a; Trudgill & Cotess, 1983; Been & Schomaker, 1986). The evidence, therefore, strengthens the hypothesis that increased concentrations of ABA, induced directly by PCN root damage or indirectly by water stress, stimulated root growth to the detriment of shoot growth.

5.6.5 Leaf area

The leaf area was measured in glasshouse grown plants at 47 DAP and field grown plants at 57 DAP for reasons previously discussed. In the glasshouse experiment, plants from oxamyl treated pots had significantly ($P = 0.009$) higher leaf area (cm^2) than all plants from pots not treated with oxamyl. This is a normal response where plants heavily-infected with PCN come from oxamyl treated plots (Evans, 1982a; Van Oijen *et. al.*, 1995; De Ruijter, 1998) but, also contradicts the root invasion analysis, which showed no treatment differences, and adds weight to the suggestion that some early benefit had been derived by the plant, for unknown reasons, from oxamyl application. Plants from the Std (control) treatment also attained significantly ($P = 0.011$) greater leaf area than plants which had received supplementary P. These trends were similar but non-significant in the field experiment, with the exception of the low rate of foliar P (Std + FP1) which attained the same leaf area as the Std (control). The trends also run parallel to the total, upper-plant and root fresh-weights. Had the plants been shown to have significantly lower P concentrations, supplementary P applications would be expected to increase leaf area during early plant growth (Freeden, Rao & Terry, 1989). Similarly, where PCN root damage had induced P deficiency, applying supplementary P to the foliage, unlike additions to the soil, would be expected to by-pass the damaged root system, ameliorate the deficiency and thus stimulate leaf expansion. This is further evidence, therefore, to suggest that the small reduction of P concentration, found within the heavily-infected Std (control) plants, was not solely responsible for the reduced plant growth. The depression of leaf area in the glasshouse, from both quantities of foliar P application, as opposed to no effect from the low quantity applied in the field, can be explained by the degree of leaf damage associated with the P application. Observations made after the foliar applications showed that increasing quantities of foliar applied P in the glasshouse gave increasing severity of leaf damage. In the field experiment, however, the lower quantity of foliar P (Std + FP1) caused no leaf damage and the higher quantity (Std + FP2) caused only minor damage. The higher levels of leaf damage occurring in glasshouse grown plants can arise from faster P uptake (Barel & Black, 1979a), which is correlated to leaf cuticle wax thickness (Lewis & Kettlewell, 1993) and which is greater in field grown plants (Van Volkenburgh & Davies, 1977). Any reduction of active leaf area then reduces photosynthetic area, dry matter production and ultimately plant growth. As the low rate of supplementary foliar P did not reduce leaf area to less than that seen in the Std (control), it is doubtful that the suggestion of an N and P interaction influenced by the soil type (Boyd & Dermott, 1967) was responsible for the reductions of plant growth in these experiments. Van Oijen *et al* (1995) speculated that hormonal responses to PCN infection could be responsible for decreases in specific leaf area. Although increased levels of cytokinins can reduce leaf area, they also produce under-developed root systems (McGaw, 1995), a feature not seen in these experiments. Increased levels of ABA, however, can reduce shoot growth in favour of root growth and could be responsible for the reduced leaf area seen in plants heavily-infected by PCN.

5.6.6 Plant nutrient status

i) Field grown plants at 30 DAP

As the 1997 experiments had shown plant emergence was significantly slower in plots not treated with oxamyl, it was hypothesised that PCN invasion of pre-emergent or early post-emergent plants could be restricting nutrient uptake. If this was shown to be the case, the application of supplementary nutrients to rectify the deficits would have to be made sufficiently early to promote rapid early growth. The nutrient status of whole plants grown in the field was determined at 30 DAP when 82% of the plants had emerged and sufficient time had elapsed for root invasion to have occurred. Although substantial PCN infection was shown in plants from plots not treated with oxamyl, no significant reductions of P concentration were found. There were, however, significantly lower concentrations of both N and K ($P = 0.043$ & $P = 0.006$, respectively) within the heavily-infected plants. The overall hypothesis that nutrient uptake is reduced by PCN infection of pre-emergent or early post-emergent plants is, therefore, supported. The results suggest that the reliance on soil P is possibly not as great as that for soil N and K during this growth period. Moorby (1968) showed that in the first 10 to 15 DAP there is an appreciable loss of N (36%) and K (17%) from the mother tuber, but that 57% of the P is lost. The importance of nutrient supply to the pre-emergent plant from sources other than the mother tuber, however, were also reported by Moorby (1968). These results suggest that if increased amounts of N and K had been applied to the soil in these experiments they could have benefited early crop growth. However, the 1997 experiment investigated the effect of increasing quantities of seed-bed N at planting and showed that, although it increased the N concentration within the plant, there was no benefit to plant emergence or early growth.

ii) Glasshouse plants at 47 and field grown plants at 57 DAP

In contrast to the nutrient concentrations at 30 DAP, there were no significant reductions of N and K concentration at 47 and 57 DAP within plants heavily-infected by PCN in either the glasshouse or the field experiment. In the field experiment the concentration of P within plants was reduced by PCN infection, as shown in the Std (control), and this was not improved by applying supplementary granular P or by applying the higher quantity of foliar P (Std + FP2). Where supplementary foliar P was applied at the lower quantity (Std + FP1), however, the P concentration deficit between the Std (control) and the lightly-infected (Std + O) was reduced by half. In contrast, both types and quantities of supplementary P application in the glasshouse experiment gave increased plant P concentrations. When the supplementary P was applied by the foliar route, the P concentrations within the plants rose to a greater concentration than found in the lightly-infected (Std + O) plants. These conflicting results emphasise how glasshouse studies, if used for preliminary investigations, can provide misleading information on which to base further research, in particular the progression into the field. It would appear from the glasshouse plant nutrient concentrations that either method of supplying supplementary P would increase the concentration of P within PCN-infected plants, but this was not so when supplementary P was applied as a broadcast granular to field grown plants. Trudgill (1980) also used the same soils in both glasshouse and field investigations and showed comparable responses: the P concentration within PCN-infected glasshouse grown plants was increased from 0.23 to 0.32% (in the dry matter of leaves) by increasing the granular P application three-fold, but in the field experiment the P concentration within PCN infected plants, although significantly increased by the triple rate P application, was only increased by a maximum of 0.02%. It was also reported by Trudgill (1980) that the three-fold P application in the field experiment increased the available soil P by only 3%. Unfortunately, no measurements were reported of available soil P for the corresponding glasshouse experiment and no causes for the low increase of available soil P were discussed. However, Haverkort & Trudgill (1995) refer to the work of Trudgill (1980) and suggest that the poor response of the field-grown plants, to the three-fold P application, probably arose from P adsorption in the heavy clay soils. This suggestion would be feasible except that the soils used by Trudgill (1980) were given as sandy loams which contain only a maximum of 20% clay (Brady, 1984). Additionally, as the same soils were used in both the glasshouse and field experiment, both soils would possess the same adsorption capacity and a similar adsorption of P in both experiments would be expected. Irrespective of these suggestions, however, my 1998 experiments used the same field soil for the glasshouse and field experiments. The soil type was a sandy loam, low in clay content, but with a pH of 7.9. Brady (1984) states that when P is applied as concentrated superphosphates to an alkaline soil (e.g. pH 8.0) the $H_2PO_4^-$ ion quickly reacts to form less soluble compounds which decreases the availability of P to the plants. One suggestion, therefore, is that the pH of the field soil caused rapid transformation of the broadcast granular P (applied as concentrated superphosphates) into poorly soluble compounds and, thus, no additional benefit was gained from these supplementary applications. De Ruijter (1998) has also shown that plant P concentration is enhanced to a greater degree in PCN-infected plants by the application of P fertilisers at soil pH 4.0 than at soil pH 6.0. Where the same soil at the same pH was used in my experiments, however, the maintenance of a greater soil moisture, from regular watering, in the glasshouse experiment would have increased the solution of the granular P (Huffman & Taylor, 1963). This may have added to the available soil P at a higher rate than transformation to insoluble P was occurring. A second explanation, however, relates simply to the differences of root growth between the two experimental environments. The application and subsequent incorporation of fertiliser granules within field soil distributes the granules in a relatively uniform pattern throughout the cultivated soil profile (Lewis, 1994). In a field situation, therefore, some of the granular P will be above the main root system of the plant. If, however, the cultivated soil, containing the granular P, is removed from the field and placed into glasshouse pots, the constrained plant root system that develops in the pot will always be in close proximity to the readily-soluble applied P and thus a greater P uptake is likely.

5.6.7 Field experiment tuber yield at 118 DAP

As the glasshouse experiment was terminated at 47 DAP, only the final yield of the field experiment will be discussed here. Oxamyl applied pre-planting to plots significantly improved the total, ware and 60 to 80mm grades of tubers ($P < 0.001$ in all cases). Whitehead *et al.* (1986) and Barker *et al.* (1998) found, with similar levels of PCN soil infestation, yield reductions of 9.6 and 19.7%, respectively, with Estima in soil not treated with oxamyl. The differences in their results may be due to the soil types, peaty loam versus clay silt loam, but Whitehead *et al.* (1986) do not specify the actual infestation level beyond 'moderate', whereas Barker *et al.* (1998) specify 32 to 34 eggs/g soil. The benefit to the plant yield in these experiments from the oxamyl application arose solely from a significant ($P = 0.001$) increase in the number of tubers collected in the 60 to 80mm grade. Applying supplementary P to plants heavily-infected with PCN produced lower tuber yields, though not significantly, than found in the Std (control) plots. It is possible that the yield reductions from the supplementary P arose from an N and P interaction as referred to earlier (Boyd & Dermott, 1967). In the absence of PCN a yield improvement from supplementary P would be small (Birch *et al.*, 1967) at the ADAS soil P index 5 (Anon, 1994) used in this experiment, although Lewis (1994) has shown non-significant yield increases and decreases from supplementary foliar P applied to plants grown in soil at 126 mg/l P (ADAS index 4; Anon, 1994). Where a moderate infestation of PCN is present, the addition of supplementary P would be expected to ameliorate the PCN-induced P deficiency reported from the 1997 experiments and by several others (e.g. Trudgill, 1980; De Ruijter, 1998). There were no significant reductions of plant P concentration arising from PCN infection at 30 DAP, however, suggesting that no rectification of a deficiency was required. The plant P concentrations were lower within PCN infected plants by 57 DAP and may have developed to a deficiency at a later stage, possibly after the termination of the foliar P programme. Trudgill (1980) also found no real yield benefit from applications of three times the standard quantity of broadcast granular P but still concluded that both N and P were most likely to be limiting the growth and yield of PCN-infected plants. One of the aims of these experiments was to investigate the potential of supplementary foliar P to by-pass the PCN damaged root system and thus provide the necessary P to the plant. This method of P application did not, however, provide any benefit to the crop yield although the lower application rate (Std + FP1) did increase the plant P concentration beyond that found in the Std (control) plants. It has been shown, therefore, that even where the plant P concentration of PCN infected plants was increased the tuber yield and tolerance of the plant was not improved.

An important determinant of the final tuber yield of potato plants is the leaf area and leaf area duration (Gunasena, 1969; MacKerron & Waister, 1985). Furthermore, Moorby & Milthorpe (1975) state that a basic underlying physiological feature is that, with any one cultivar, the smaller the leaf area at tuber initiation the slower the rate of tuber bulking and the lower the final tuber yield. Therefore, it is not surprising that the final tuber yield is correlated with the leaf area measurement at 57 DAP. It is, however, surprising that the supplementary P caused an overall reduction of leaf area as Dyson & Watson (1971) report that P applications improve leaf area. Marschner (1995) suggested that P deficiency will decrease leaf growth rate, and therefore leaf area, which would suggest that where plant P concentrations were increased by foliar applications (e.g. Std + FP1) there would be an improvement in leaf area. A further consideration, in relation to the final tuber yield and the reduced leaf area, however, is the importance of an adequate N supply in promoting leaf expansion (Vos & Biemond, 1992). The significantly lower N concentration reported in these experiments at 30 DAP may, therefore, have prevented a response to the supplementary P applications and ultimately led to lower crop yields.

i) Covariance analysis and tuber yield

The importance, relevance and application of covariance analysis to experiments with PCN were discussed earlier (section 4.7.10) and outlined the problems of using the initial PCN population density as a covariate when oxamyl was also used in these experiments. It was, therefore, suggested that root invasion data provided a more suitable covariate for adjusting the treatment means to account for the variations in stress imposed by different levels of PCN infection. The covariate analysis of total tuber yield showed that root invasion values at 30 DAP had a significant covariate effect and, consequently, the tuber yields were adjusted to show no significant effect from the oxamyl application. The initial PCN population density and root invasion values at 57 DAP, however, showed no covariance significance. One of the underlying assumptions of covariate analysis, however, is that the variable used as the covariate is known (proven) to be linearly related to the primary variable being analysed (Gomez & Gomez, 1984). These results support the 1997 findings that no relationship was demonstrated, in an experiment that included nematicide treatments, between the initial PCN population density and the final crop yield, but that significant relationships exist between the root invasion and final crop yields. The strength of the relationship, however, was shown to be far greater with root invasion values at 30 DAP ($r^2 = 0.71$) than at 57 DAP ($r^2 = 0.23$). In addition to these analyses, it is appropriate to use logarithmic data transformation where some of the observed values are small in comparison to the others. In this way it is possible to attain a more suitable statistical model for parametric analysis (Gomez & Gomez, 1984; Pearce *et. al.*, 1988). The $\log_e$ transformed root invasion data explained the relationship between root invasion and tuber yield at 30 DAP less well ($r^2 = 0.52$) but slightly improved the relationship at 57 DAP ($r^2 = 0.28$). It is suggested, therefore, that untransformed root invasion is the most suitable covariate when the root invasion analysis is carried out at 30 DAP or 57 DAP. These results agree with those of 1997, that root invasion is the only suitable covariate for use in these experiments.

ii) Tuber dry matter content

In contrast to the 1997 experiments, the application of oxamyl to plots significantly ($P = 0.002$) reduced the dry matter content of tubers. As the plants in oxamyl treated plots had not senesced, in contrast to those in plots not treated with oxamyl, the early defoliation and harvest of oxamyl treated plots would give rise to lower dry matter contents (Storey & Davies, 1992). There were small but non significant effects on the tuber dry matter arising from supplementary P applications. This agrees with the findings of Lewis (1994), where increased applications of broadcast granular, placed-liquid and foliar P applications showed small non-significant effects.

5.6.8 Comparing glasshouse and field investigations

It has been shown to varying degrees in these experiments why results from glasshouse investigations can lead to inappropriate choice of treatments for fieldwork. The most notable effect seen in the glasshouse was the ability of both broadcast granular and foliar P applications to increase the plant P concentration. Although it is possible to mimic the environmental parameters to some degree, e.g. matching the temperature fluctuations and soil moisture, it would be difficult to create a glasshouse environment which adequately represents the outdoor environment. Legg (1989) suggests that glasshouse-grown plants experience lower light intensity, higher humidity, less air disturbance and smaller extremes in temperature than outdoor-grown plants. In the field situation, therefore, the plant leaf would encounter wind and the abrasive products carried within it, thus encouraging thicker cuticle wax, whilst in the absence of soil compaction, the roots would have access to greater volumes of soil. A second consideration for experiments with PCN relates to the quantity of PCN inoculum present in the investigations. Trudgill (1980) suggested that the greater quantity of PCN inoculum in the field gave the potential for a more prolonged attack on the plant roots than the equivalent PCN density in glasshouse pots. The extent to which this would be a problem would depend on the size of the pot and the duration of the experiment and, therefore, the size of the root system. However, the large root system found in this glasshouse experiment would have very quickly explored and depleted the PCN inoculum available to it. The disparities of uptake of leaf-applied nutrients between glasshouse and field grown plants probably arose from differences of cuticular wax thickness. Scheiferstein & Loomis (1956) report that the rate of solute penetration is correlated inversely with cuticle thickness, which agrees with Fick's second law of diffusion where the time for diffusion increases with the square of the distance (Noble, 1991). Therefore, as Van Volkeburgh & Davies (1977) have demonstrated that field grown plants have thicker cuticles than plants grown in controlled environments, a more rapid uptake of foliar applied P would be expected in the glasshouse plants. Additionally, glasshouse grown plants experienced higher daytime temperatures than the field grown plants and an accompanying increase of solution penetration due to decreased cuticular wax viscosity would occur (Price, 1982). Unfortunately, this would also increase the speed of nutrient uptake and thus the severity of the leaf damage (Barel & Black, 1979a). Therefore, as the severity of leaf damage from foliar P applications was much greater on the glasshouse plants than on the field grown plants, a more rapid and greater nutrient uptake must have occurred in the glasshouse plants. This type of differences are not uncommon as several workers have shown this effect with many agrochemicals (Hewitt *et al.*, 1994).

5.6.9 Conclusions

Despite the indications from the 1997 experiments that P deficiency during the pre- or early post-emergent plant growth could be responsible for delaying the growth of PCN-infected plants these experiments did not provide evidence to support this. The application of supplementary P did not increase the tuber yield or plant tolerance of PCN infection. There was evidence, however, that very early foliar P applications could increase concentrations of P within plants grown both in the glasshouse and the field, but it was clearly shown that increasing the plant P concentration did not encourage plant growth. There was, however, evidence to suggest that foliar P applications are suitable to increase the P concentration of plants infected by PCN even when the ground cover gives a small spray target. As N and K concentrations were greatly reduced in the pre-emergent field grown plants they may have been limiting plant growth. However, as no benefit to early plant growth was seen in 1997, when all of the recommended N was applied at planting, this may suggest that two or more nutrients need to be supplied to enhance early plant growth. The two experiments in 1998 showed that glasshouse experiments can mimic some aspects of field-grown plants but that the uptake and final plant P concentrations were greatly influenced by their growing environments. It is suggested, therefore, that using the results of preliminary glasshouse investigations are treated with caution when used as a basis for field investigations. These findings are supported by the work of Trudgill (1980), who outlined the differences seen between glasshouse and field experiments and emphasised the need for field experimentation as the main type of investigation in this type of research. Although a separate mechanism, e.g. the influence of ABA, would explain the lack of response to supplementary P applications, the growth improvement of glasshouse plants shown by Trudgill (1980) would dispute this theory. However, as there were no measurements of ABA concentrations for these experiments this is one possible explanation.

6. Nutrient ratios

6.1 Introduction

Nutrient ratios were first proposed by Beaufils (1957) as a useful technique to aid the interpretation of nutrient disorders in plants. The technique is based on the analysis of nutrient concentrations in plant tissues from which the relationship between nutrients can be investigated. Many plant samples are collected for nutrient analysis from high yielding crops grown under commercial conditions in order to provide data from which nutrient ratios that can be classed as normal values (norms) can be determined, e.g. the ratio of N to P, N to K and K to P. Nutrient ratios from low yielding crops can then be compared to the 'norm' values by the use of specific interpretation methods. These comparisons allow the identification of nutrients which fall within specific parameters of balance, limitation or excess, in comparison to 'norms', thus highlighting potential nutrient disorders in the low yielding plants. One method, known as the Diagnosis and Recommendation Integrated System (DRIS), is especially useful in the interpretation of nutrient disorders in plants because it is less affected by plant ageing than the more commonly used critical or deficiency values (Sumner, 1977; Walworth & Sumner, 1987), and so moderates the differences between cultivars and environments (Gascho, Anderson & Bowen, 1993).

A review of the literature concerning the effects of PCN on the nutritional status of infected potatoes has revealed records of reduced uptake of N, P and K (Trudgill *et al.*, 1975b; Van Oijen *et al.*, 1995; De Ruijter, 1998). Previous work in this area, however, has produced inconsistent results as to which, if any, nutrients were limiting crop yield of PCN infected potatoes; e.g. Trudgill *et. al.* (1975a) suggest that N did not seem to be a growth limiting factor, whereas Haverkort *et al.* (1994) suggest that N could be a growth limiting factor. The reduced nutrient uptakes and/or deficiencies that have been reported were identified either by statistical analysis, where nutrient values from PCN infected plants are compared with values for non-infected plants, or by comparison of the concentrations with published values for nutrient sufficiency or deficiency. I have used the DRIS nutrient diagnosis method in an attempt to interpret nutritional disorders of PCN infected plants. Unlike the normal DRIS method, however, I have used values for high yielding plants taken from experimental plots treated with oxamyl. This allowed the comparison and interpretation of nutrient concentrations for heavily- and lightly-infected plants of the same cultivar grown in the same environment in each experiment.

The inclusion of the nutrient ratio analysis as a separate chapter, as opposed to its inclusion within individual experiments, is for two reasons: 1) nutrient ratios were investigated as part of a continuing literature review midway through the second year's experimental work, and their inclusion in the 1996 results could lead the reader to question why they were not a consideration in the design of the 1997 experiments, and 2) it was felt that the 1998 investigations should continue to use statistical differences in nutrient concentrations whilst at the same time providing data to further assess nutrient ratios as a diagnostic tool for PCN infected plants.

6.1.1 The importance of nutrient balance

In the absence of nematodes, the complex interactions occurring between nutrients are well documented, illustrating how interactions can occur in both the soil and plant cell environments. N applications made in the absence of adequate supplies of K can not only result in low crop yields but, as the N supply increases, yield depression is accentuated (Marschner, 1995). The form of N applied to the soil can also influence the uptake of P. Where N is applied as ammonium (NH_4^+) the soil pH will be different from where it is applied as nitrate (NO_3^-), which can affect P uptake as the mechanism for this is pH dependent (Mengel & Kirkby, 1987). N and P concentrations within the plant are also responsible for non-specific interactions. Where the concentration of either N or P is increased, the concentration at which the other nutrient would become critically deficient is also increased (Marschner, 1995). In addition, as concentrations of K increase within the plant Mg deficiency will occur first, followed by Ca deficiency if the K concentration continues to rise (Benton-Jones *et al.,* 1991). These deficiencies are the result of cation competition and arise because the uptake of the nutrients is governed by the cellular binding strengths of the ionic nutrient forms, of which K^+ is the strongest, followed by Ca^{2+} and, most weakly, Mg^{2+} (Marschner, 1995). Although some of the enzyme activation roles of Mg^{2+} can be filled by K^+ the essential function of Mg^{2+} in protein synthesis cannot be replaced and, at excessive K^+ concentrations, protein synthesis will cease. K deficiency is also associated with a low ratio of organic to inorganic P and an increased uptake of P. This deficiency is thought to inhibit the pyruvic kinase enzyme, which controls the reversible formation of ATP (adenosine triphosphate), and as ATP utilisation is prevented, the concentration of inorganic P is affected (Hewitt & Smith, 1975). These examples of specific or non-specific nutrient interactions illustrate how the concentration of one nutrient can adversely affect the concentration of other nutrients and, ultimately, plant growth.

6.2 General materials and methods

The materials and methods for the individual experiments are given in the relevant sections of this thesis: 1996, 1) the effects of fertiliser application type and foliar NPK on the growth and yield response of potatoes infected by the potato cyst nematode *G. pallida* , 2) the effects of individual and combined applications of foliar N. P and K on the growth and yield response of potatoes infected by the potato cyst nematode *G. pallida* , section 3.2; 1997, 1) the growth and yield responses to supplementary foliar nitrogen and foliar phosphate of potatoes infected by potato cyst nematodes, 2) the growth and yield responses to supplementary foliar nitrogen of potatoes infected by potato cyst nematodes, 3) the growth and yield responses to basal, tuber initiation and supplementary foliar nitrogen of potatoes infected by potato cyst nematodes, section 4.2; 1998, 1) the growth and yield response of field grown potatoes to supplementary broadcast granular or foliar applied phosphate when infected by potato cyst nematodes, 2) the growth response of glasshouse grown potatoes to supplementary broadcast granular or foliar applied phosphate when infected by potato cyst nematodes, section 5.2.

6.2.1 Calculation and interpretation of nutrient ratios

A brief summary of the methods of nutrient ratio analysis follows. For more specific and detailed methodology see Sumner (1977), Meldal-Johnsen & Sumner (1980) and Walworth & Sumner (1987).

i) Sample collection, analysis and ratio definition

Whole plant samples, collected primarily for plant growth and PCN root invasion analysis within individual experiments, and fourth leaf samples, collected solely to determine nutrient concentrations, were used for this work with nutrient concentrations analysed as described in chapter 2.1. The N, P and K concentrations were expressed in three forms of product, i.e. N/P, N/K, K/P; P/K, P/N, K/N; or NP, NK, PK. The form of expression which resulted in the highest variance ratio between the oxamyl treated control plants and the PCN infected plants was selected as the most appropriate for comparison of the nutrient ratios (Walworth & Sumner, 1987). In all of the experiments considered, the form of expression to meet this criterion was N/P, N/K and K/P. The nutrient concentrations were converted to ratios for plants or leaves for each plot, with the oxamyl treated control values forming the basis of the

DRIS interpretation chart.

ii) Nutrient chart

The nutrient chart (Figure 6.1) comprises three intersecting axes, one for each ratio, with the point of intersection corresponding to the mean ratio values for the high yielding plants or, in this case, the plants from oxamyl treated plots. These mean values represent the best estimate of the optimum plant nutrient composition to obtain a high yield. As single values are inflexible, however, two concentric circles are added to the chart to provide a range of values depicting nutrient balance, limitation or excess. The diameter of the first circle is set at 4 times the standard deviation of the values making up the mean ratio divided by 3 (4SD/3), and that of the second at 8SD/3 (Beaufils, 1971). Values within the inner circle represent the range of ratios over which the nutrients are in balance and are depicted by an horizontal arrow →; values falling between the inner and outer circles represent moderate imbalance and are depicted by a 45° arrow ↘ or ↗; values falling outside the outer circle represent serious imbalance and are depicted by a vertical arrow ↑↓. To illustrate, the DRIS chart interpretation in Figure 6.1 shows nutrient indices for one of the experiments. The mean value on the N/P axis is 11.49, the inner circle diameter is 2.46 and the outer circle diameter is 4.92. This gives an in-balance range of 10.26 to 12.72, a moderate imbalance either between 12.72 and 13.95 or between 10.26 and 9.03, and a marked imbalance where the ratio is greater than 13.95 or less than 9.03. If an N/P ratio from a PCN infected plant (or any other sample) were calculated at 13.0, a moderate P limitation would be indicated.

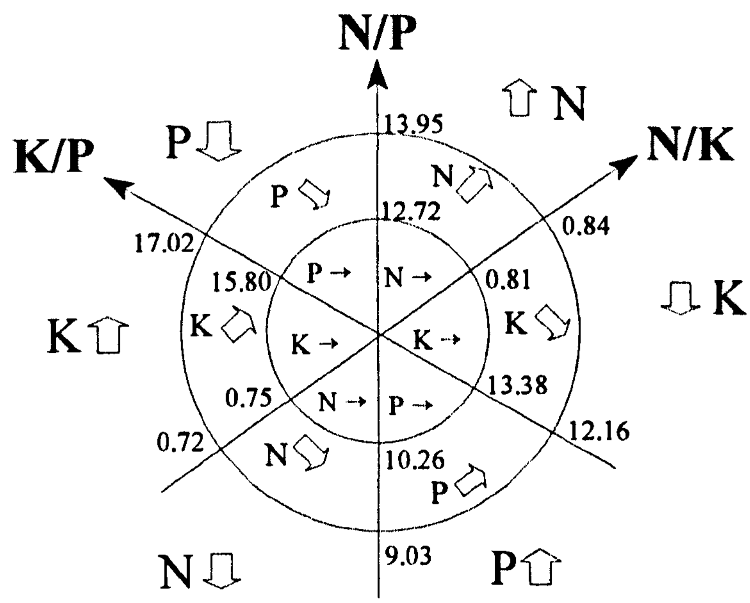

Figure 6.1. DRIS chart for determining the nutrient balance and qualitative order of requirement for N, P and K in the potato cultivar Pentland Dell at 69 days after planting in an investigation of the effects of fertiliser application type, foliar NPK and nematicide of potatoes infected by *G. pallida*.

For each sample, the three ratios are checked against the appropriate axis on the chart and the nutrients and symbols noted accordingly. For ratios N/P of 13.0, N/K of 0.82 and K/P of 12.20, therefore, the assignations would be : N/P = P ↘, N/K = K ↘, and K/P =. K ↘. Any nutrient not shown to be out of balance is assigned a balance, therefore N = →. With this sample, the qualitative order of nutrient requirement is K > P > N to bring the plant into balance. On each axis there are both positive ↗ and negative ↘ arrows but, although it is possible to suggest that a nutrient is in excess it is not possible to remove the nutrient from the plant and, therefore, only the negative ↘ assignations are considered in terms of remedial nutrient applications.

iii) Nutrient indices

Although the DRIS chart is simple to construct and interpret, problems arise when two nutrients are assigned the same degree of imbalance, e.g. N $\searrow$ and K $\searrow$, as there is no way of deciding which nutrient is most out of balance. For this purpose, a mathematical approach resolves the ratios into individual nutrient indices which are based on the relationship of the sample ratios to norm ratios (Walworth & Sumner, 1987). The resulting values are then a quantitative representation of the balance of the nutrients under study. In an example where N/P = P $\searrow$, N/K = K $\searrow$, and K/P = K $\searrow$ and the final assignation would be K $\searrow$ P $\searrow$ N $\rightarrow$, the indices could resolve this into N = 12, P = -4 and K = -8, giving K as much more out of balance than P. It should be noted that for any group of indices the total values should always equal zero, which is equilibrium.

Two points are worthy of note here, 1) even where a minus value is indicated this does not specify a definitive nutrient deficiency but a potential nutrient limitation in respect of its balance against a normal high yielding plant, and 2) to gain the most insight into the potential nutrient disorder within the plant, as many nutrients as practical should be included in the analysis.

6.3 Results

6.3.1 Experiment one 1996

The effects of fertiliser application type and foliar NPK on the growth and yield of potatoes infected by the potato cyst nematode, *Globodera pallida*.

The treatment chosen as most representative of a high yielding (norm) plant population was the broadcast fertiliser application in plots treated with oxamyl. Calculated ratios for the norms and plants from plots not treated with oxamyl are given in Table 6.1. The interpretation of the DRIS chart (Figure 6.2 and Table 6.2) suggests that where all of the fertiliser was applied as a broadcast granular, in the absence of oxamyl, K was limiting. This limitation was removed when the fertiliser was split between broadcast granular and foliar NPK applications, and the concentrations were in balance. Where all of the fertiliser was applied as liquid placed fertiliser nutrients were again in balance, whereas splitting the fertiliser between liquid placed and foliar NPK gave rise to an N limitation. Unexpectedly, plots which had received no fertiliser or oxamyl were shown to be in nutrient balance. DRIS nutrient indices (Table 6.2), however, show that where all the quantity of fertiliser was applied as broadcast granular the order of nutrient requirement was K followed by P. Furthermore, when the fertiliser was split between broadcast granular and foliar NPK, a moderate N and K limitation existed, unlike the balance suggested by the DRIS chart. Again in contrast to the DRIS chart, where all of the fertiliser was applied as liquid placed, N was shown to be the limiting nutrient, whereas splitting the fertiliser between liquid placed and foliar NPK confirmed an N limitation in both systems of analysis.

Nutrient indices showed that where no fertiliser had been applied, or where all of the fertiliser had been applied as a broadcast granular, K was the most limiting nutrient and the lowest tuber yields were attained. However, where higher tuber yields were recorded from plots to which the fertiliser was applied as broadcast granular plus foliar NPK, all liquid placed, or liquid placed plus foliar NPK, the most limiting nutrient was N (Table 6.2).

Table 6.1. Nutrient ratios calculated for nutrient concentrations at 69 DAP (four days after the second foliar application) within whole potato plants arising from treatments of fertiliser application type and foliar NPK to potato plants infected by *Globodera pallida.*

	N/P	N/K	K/P
'norm'[a]	11.49	0.79	14.59
NF[b]	11.25	0.79	14.10
BF	11.89	0.82	14.45
BF+F	10.94	0.78	14.05
LF	10.34	0.75	13.81
LF+F	10.04	0.75	13.40

[a] broadcast granular fertiliser plots treated with oxamyl pre-planting

[b] for fertiliser application methods for plots not treated with oxamyl, see Table 3.1.

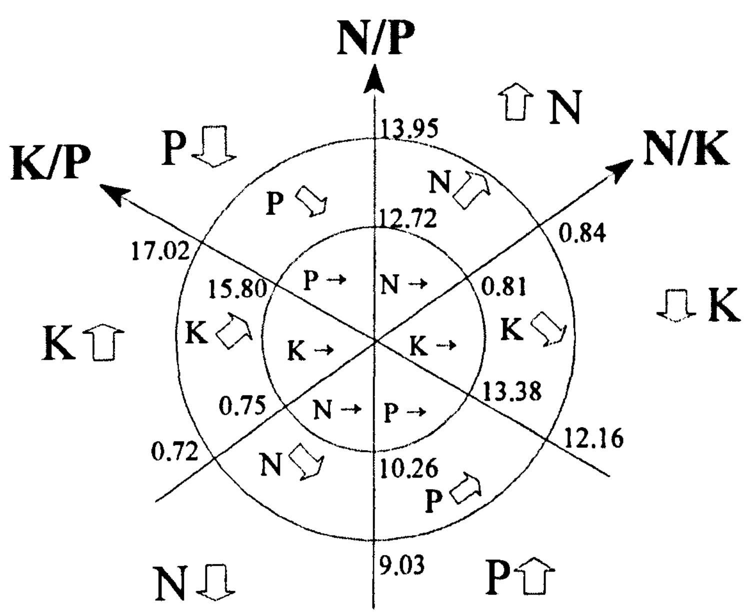

Figure 6.2. DRIS chart for the interpretation of nutrient ratios calculated from plant nutrient concentrations at 69 DAP (four days after the second foliar application) of whole potato plants arising from treatments of fertiliser application type and foliar NPK to potato plants infected by *Globodera pallida,*.

Table 6.2. DRIS chart and index interpretation of the effects of fertiliser application type, foliar NPK and nematicide on the nutrient ratios calculated from nutrient concentrations within whole potato plants at 69 DAP (four days after the second foliar application) of potatoes infected by *Globodera pallida* .

	Chart[a]	In[b]	Ip[c]	Ik[d]	Ranking[e]	Total yield (t/ha)
'norm'[f]	N→ P→ K→	0	0	0	N = P = K	34.3
NF[g]	N→ P→ K→	1	2	-3	K > N > P	24.9
BF	K↘ N→ P→	6	-1	-5	K > P > N	32.7
BF+F	N→ P→ K→	-2	4	-2	N = K > P	33.8
LF	N→ P→ K→	-7	6	1	N > K > P	34.6
LF+F	N↘ P→ K→	-8	8	0	N > K > P	34.2

[a] nutrient balance derived from the DRIS chart; [b] nitrogen index; [c] phosphate index; [d] potassium index; [e] order of nutrient requirement; [f] broadcast granular fertiliser plots treated with oxamyl pre-planting; [g] for fertiliser application method for plots not treated with oxamyl, see Table 3.1.

6.3.2 Experiment two 1996

The effects of individual and combined applications of foliar NPK on the growth and yield of potatoes infected by the potato cyst nematode, *Globodera pallida*.

The treatment chosen as most representative of a high yielding (norm) plant population was the standard fertiliser application in plots treated with oxamyl. Calculated ratios for the norms and plants from plots not treated with oxamyl are given in Table 6.3. A DRIS chart interpretation and the calculated nutrient indices (Figure 6.3, Table 6.4) suggested that P was limiting growth in the majority of plants from plots not treated with oxamyl. DRIS charts suggested that the application of foliar KP resulted in a better nutrient balanced plant but nutrient indices generally highlighted P as a limiting nutrient. The specific order of nutrient limitation was the same irrespective of a high or low final yield (Table 6.4).

Table 6.3. The nutrient ratios calculated from plant nutrient concentrations 82 DAP of whole potato plants arising from individual and combined applications of foliar nutrients to potato plants infected by *Globodera pallida*,.

	N/P	N/K	K/P
'norm' [a]	11.79	0.67	17.79
Std + FW [b]	12.53	0.64	19.67
Std + Fol N	12.94	0.66	19.46
Std + Fol P	13.85	0.68	20.46
Std + Fol K	13.05	0.64	20.32
Std + Fol NP	12.57	0.64	19.56
Std + Fol NK	13.75	0.64	21.35
Std + Fol KP	11.89	0.62	19.01
Std + Fol NPK	12.73	0.67	19.31

[a] treated with oxamyl pre-planting

[b] for foliar applications for plots not treated with oxamyl, see Table 3.2.

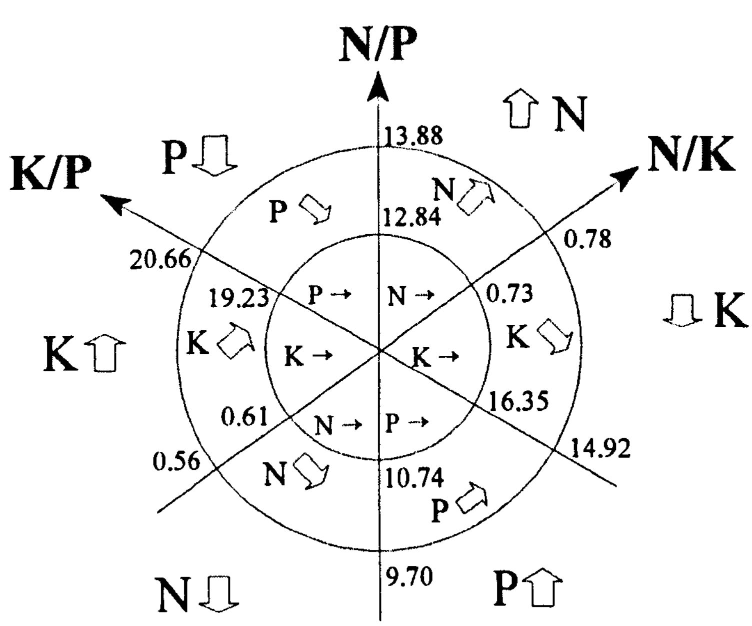

Figure 6.3. DRIS chart for the interpretation of nutrient ratios calculated from plant nutrient concentrations at 82 DAP of whole potato plants arising from individual and combined applications of foliar nutrients to potato plants infected by *Globodera pallida*.

Table 6.4. DRIS chart and index interpretation of the effects of individual and combined applications of foliar nutrients on the nutrient ratios calculated from nutrient concentrations at 82 DAP of whole potato plants of potatoes infected by *Globodera pallida.*

	Chart[a]	In[b]	Ip[c]	Ik[d]	Ranking[e]	Tuber yield (t/ha)
'norm'[f]	N→P→ K→	0	0	0 [f]	N = P = K	42.8
Std + FW [g]	P↘ N→ K→	0	-7	6	P > N >K	38.4
Std + Fol N	P↘ N→ K→	2	-8	5	P > N >K	43.9
Std + Fol P	P↘ N→ K→	7	-13	6	P > K >N	36.4
Std + Fol K	P↘ N→ K→	2	-10	8	P > N >K	38.1
Std + Fol NP	P↘ N→ K→	1	-7	6	P > N >K	38.7
Std + Fol NK	P↓ N→ K→	5	-15	10	P > N >K	43.8
Std + Fol KP	N→P→ K→	-3	-3	6	P = N >K	37.0
Std + Fol NPK	P↘ N→ K→	3	-7	4	P > N >K	36.5

[a] nutrient balance derived from the DRIS chart; [b] nitrogen index; [c] phosphate index; [d] potassium index; [e] order of nutrient requirement; [f] norms treated with oxamyl pre-planting; [g] for foliar applications for plots not treated with oxamyl, see Table 3.2.

DRIS indices reflected the P limitation shown in the DRIS chart in plots not treated with oxamyl, but also suggested that, after P, N was more limiting than K. It is also worthy of note that the application of foliar P did nothing to redress the P limitation and actually appeared to increase its limitation with a corresponding excess of N.

6.3.3 Experiment one 1997

The growth and yield responses to supplementary foliar nitrogen and foliar phosphate of potatoes infected by potato cyst nematodes.

The treatment chosen as most representative of a high yielding (norm) plant population was the standard fertiliser application in plots treated with oxamyl. Calculated ratios for the norms and plants from plots not treated with oxamyl are given in Table 6.5. DRIS chart interpretation (Figure 6.4 & Table 6.6) suggests that in all plots not treated with oxamyl both P and K were severely out of balance and potentially restricting plant growth at 61 DAP. With DRIS indices, P was shown to be the most limiting and K of secondary importance. All plots showing the severe P limitation had a much reduced final tuber yields (Table 6.6). Simple linear regression showed only weak evidence that N/P (adjusted r^2 = 39.2) and N/K (adjusted r^2 = 40.2) were related to the final tuber yield, whilst K/P had no relation to yield.

At 104 DAP, the DRIS chart interpretation (Figure 6.5 & Table 6.7) suggests that, in plots not treated with oxamyl, the most limiting nutrient was K. These findings were supported by the DRIS indices (Table 6.7), which showed K as extremely out of balance. All plots showing the severe K limitation had much reduced final tuber yields (Table 6.7).

Table 6.5. Nutrient ratios calculated for nutrient concentrations from whole potato plant dry matter at 61 DAP and potato fourth leaf plus petiole at 104 DAP, arising from applications of supplementary foliar N and foliar P to potatoes infected by potato cyst nematodes.

	61 DAP			104 DAP		
Treatment	N/P	N/K	K/P	N/P	N/K	K/P
Std + O [a]	10.95	0.51	21.42	25.95	0.69	37.64
Std + FN4	12.58	0.58	21.54	25.72	0.82	31.25
Std + FN4P1	13.20	0.59	22.31	24.72	0.81	30.64
Std + FN4P2	12.83	0.58	22.31	23.81	0.79	30.14
Std + FN5	13.01	0.61	21.42	24.10	0.85	28.53
Std + FN5P1	13.73	0.59	23.19	26.36	0.86	30.70
Std + FN5P2	13.01	0.57	22.68	26.25	0.83	31.89

[a] see table 4.1.

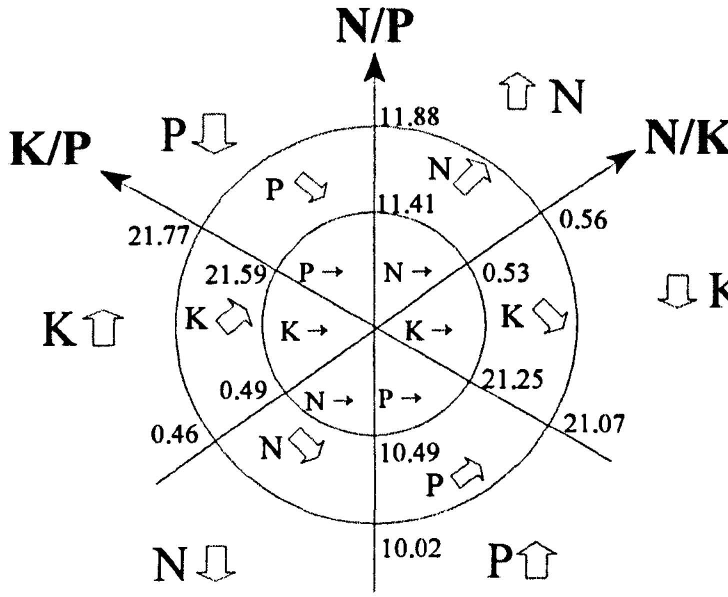

Figure 6.4. DRIS chart for the interpretation of nutrient ratios calculated for nutrient concentrations from whole potato plant dry matter, at 61 days after planting arising from applications of supplementary foliar N and foliar P to potatoes infected by potato cyst nematodes.

Table 6.6. DRIS chart and index interpretation of the effects of supplementary foliar N and foliar P on nutrient concentrations from whole potato plant dry matter (at 61 DAP) and total tuber yield of potatoes infected by potato cyst nematodes.

Treatment	Chart[a]	In[b]	Ip[c]	Ik[d]	Ranking[e]	Tuber yield (t/ha)
Std + O[f]	N→P→ K→	0	0	0	N = P = K	54.1
Std + FN4	P↓ K↓ N→	22	-14	-8	P > K > N	23.5
Std + FN4P1	P↓ K↓ N→	28	-34	6	P > K > N	28.6
Std + FN4P2	P↓ K↓ N→	24	-31	7	P > K > N	22.1
Std + FN5	P↓ K↓ N→	30	-15	-15	P = K > N	23.9
Std + FN5P1	P↓ K↓ N→	32	-55	23	P > K > N	25.5
Std + FN5P2	P↓ K↓ N→	24	-39	16	P > K > N	29.5

[a] nutrient balance derived from the DRIS chart; [b] nitrogen index; [c] phosphate index; [d] potassium index; [e] order of nutrient requirement; [f] for treatments see Table 4.1.

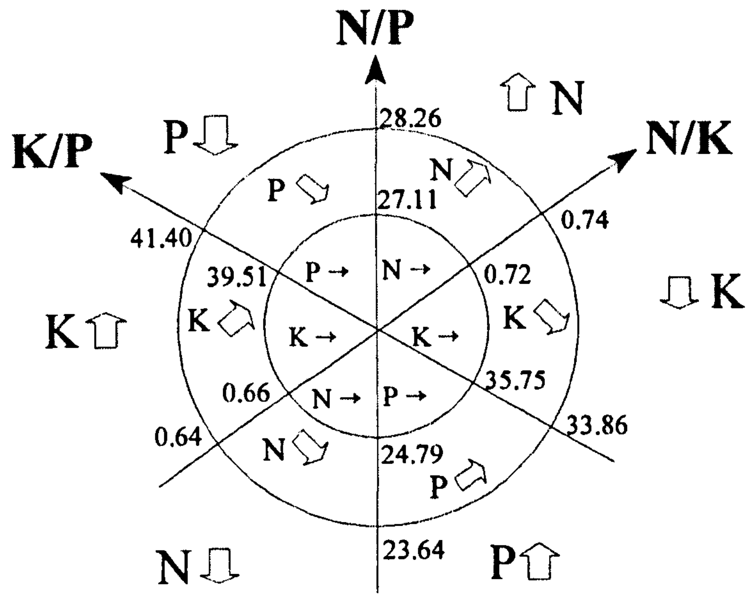

Figure 6.5. DRIS chart for the interpretation of nutrient ratios calculated for nutrient concentrations of potato fourth leaf plus petiole at 104 days after planting arising from applications of supplementary foliar nitrogen and foliar phosphate to potatoes infected by potato cyst nematodes.

Table 6.7. DRIS chart and index interpretation of the effects of supplementary foliar N and foliar P on nutrient concentrations from potato fourth leaf plus petiole at 104 DAP and total tuber yield of potatoes infected by potato cyst nematodes.

Treatment	Chart[a]	In[b]	Ip[c]	Ik[d]	Ranking[e]	Tuber yield (t/ha)
Std + O[f]	N→P→ K→	0	0	0	N = P = K	54.1
Std + FN4	K↓ P→ N→	16	14	-30	K > P > N	23.5
Std + FN4P1	K↓ N↘ P→	12	19	-31	K > N > P	28.6
Std + FN4P2	K↓ N↘ P→	6	23	-30	K > N > P	22.1
Std + FN5	K↓ N↘ P→	15	27	-42	K > N > P	23.9
Std + FN5P1	K↓ P→ N→	23	14	-37	K > P > N	25.5
Std + FN5P2	K↓ P→ N→	19	11	-30	K > P > N	29.5

[a] nutrient balance derived from the DRIS chart; [b] nitrogen index; [c] phosphate index; [d] potassium index; [e] order of nutrient requirement; [f] for treatments see Table 4.1

6.3.4 Experiment two 1997

The growth and yield response to supplementary foliar nitrogen of potatoes infected by potato cyst nematodes.

The treatment chosen as most representative of a high yielding (norm) plant population was the standard fertiliser application in plots treated with oxamyl. Nutrient ratios were calculated from nutrient concentrations within whole plant dry matter at 58 DAP, and before the application of foliar N (Table 6.8).

Table 6.8. Nutrient ratios calculated for nutrient concentrations within whole potato plant dry matter, at 58 days after planting, in an investigation of the growth and yield response to supplementary foliar nitrogen of potatoes infected by potato cyst nematodes.

	58 DAP		
treatment	N/P	N/K	K/P
Std + O [a]	10.26	0.61	16.72
Std	12.49	0.70	17.87
Std + Fol 2% N	13.08	0.75	17.38
Std + Fol 4% N	12.46	0.73	17.09
Std + Fol 6% N	12.37	0.72	17.22

[a] see Table 4.2.

DRIS chart interpretation (Figure 6.6 and Table 6.9) suggested that both P and K were distinctly out of balance and that both may have been restricting plant growth. DRIS indices (Table 6.9) suggested that P was the most limiting nutrient. Simple linear regression showed some evidence that N/P (adjusted $r^2 = 48.0$) and N/K (adjusted $r^2 = 40.1$) were related to the final tuber yield but N/K showed no relationship ($r^2 = 14.2$). All tuber yields in plots not treated with oxamyl were substantially reduced (Table 6.9).

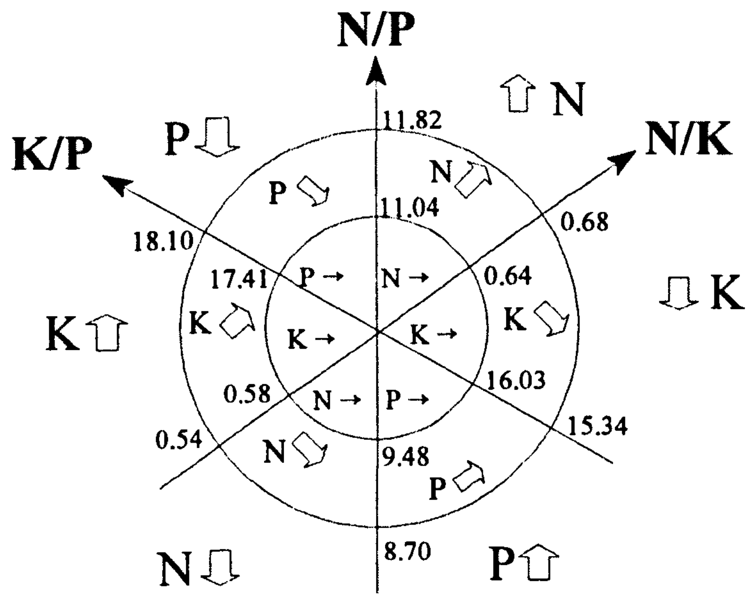

Figure 6.6. DRIS chart for the interpretation of nutrient ratios calculated from nutrient concentrations within whole potato plant dry matter, at 58 DAP in an investigation of the growth and yield response to supplementary foliar N of potatoes infected by potato cyst nematodes.

Table 6.9. DRIS chart and nutrient indices calculated from nutrient concentrations within whole plants at 58 DAP and total tuber yields in an investigation of the growth and yield response to supplementary foliar N of potatoes infected by potato cyst nematodes.

treatment	Chart[a]	In[b]	Ip[c]	Ik[d]	Ranking[e]	tuber yield (t/ha)
Std + O [f]	norm data	0	0	0	N = P = K	52.0
Std	P↓ K↓ N→	19	-15	-3	P > K > N	24.7
Std + Fol 2% N	P↓ K↓ N→	26	-15	-11	P > K > N	23.9
Std + Fol 4% N	P↓ K↓ N→	21	-11	-10	P > K > N	28.6
Std + Fol 6% N	P↓ K↓ N→	20	-11	-9	P > K > N	29.5

[a] nutrient balance derived from the DRIS chart; [b] nitrogen index; [c] phosphate index; [d] potassium index; [e] order of nutrient requirement; [f] for treatments see Table 4.2

6.3.5 Experiment three 1997

The growth and yield response to oxamyl and basal, tuber initiation and supplementary foliar nitrogen, of potatoes infected by potato cyst nematodes.

The treatment chosen as most representative of a high yielding (norm) plant population was the standard fertiliser application in plots treated with oxamyl. At 56 DAP, nutrient ratios were calculated from nutrient concentrations within the dry matter of whole plants (Table 6.10). DRIS chart interpretation (Figure 6.7 and Table 6.11) showed that P and K were the most limiting nutrients at this time. This was further clarified by DRIS indices (Table 6.11), which ranked P as the most limiting nutrient. Plants shown to have severe P limitations produced substantially lower tuber yields (Table 6.11). Simple linear regression showed some evidence that N/P (adjusted $r^2 = 51.2$), and no real evidence that N/K (adjusted $r^2 = 31.4$) and K/P (adjusted $r^2 = 29.8$) could be related to the final tuber yield.

At 107 DAP, the nutrient ratios were calculated from nutrient concentrations within the dry matter of the fourth leaf (Table 6.10). DRIS chart interpretation (Figure 6.8 and Table 6.12) showed in plots not treated with oxamyl that: 1) applying the basal N quantity as a 50/50 split between planting and tuber initiation, with no supplementary foliar N, resulted in a moderate N and K limitation; 2) where this same basal N regime was supplemented with foliar N, only K was moderately limiting; 3) where the total basal N quantity was applied at planting and tuber initiation in a 66/33 split, and supplementary foliar N was applied, the plants appeared to be nutrient balanced; 4) where all of the basal N was applied at planting and supplementary foliar N was applied, a severe P limitation occurred. These finding suggest were supported by DRIS indices (Table 6.12) which suggested that K was most limiting in all plots not treated with oxamyl except where all of the basal N was applied at planting, when P was severely limiting. Plants shown to have severe K or P limitations produced substantially lower tuber yields (Table 6.12).

Table 6.10. Nutrient ratios calculated from nutrient concentrations within whole potato plant dry matter, at 56 DAP and potato fourth leaf plus petiole at 107 DAP, in an investigation of the growth and yield response to oxamyl and basal, tuber initiation and supplementary foliar N of potatoes infected by potato cyst nematodes.

	56 DAP			107 DAP		
treatment	N/P	N/K	K/P	N/P	N/K	K/P
NORM+O [a]	9.59	0.58	16.50	23.53	0.83	28.80
NORM	11.98	0.63	18.89	22.50	0.85	26.43
NORM+F	12.19	0.65	18.86	24.26	0.91	26.71
HIGH+F	12.66	0.65	19.51	24.39	0.90	27.17
ALL+F	11.87	0.65	18.26	27.27	0.87	31.46

[a] for treatments see Table 4.3.

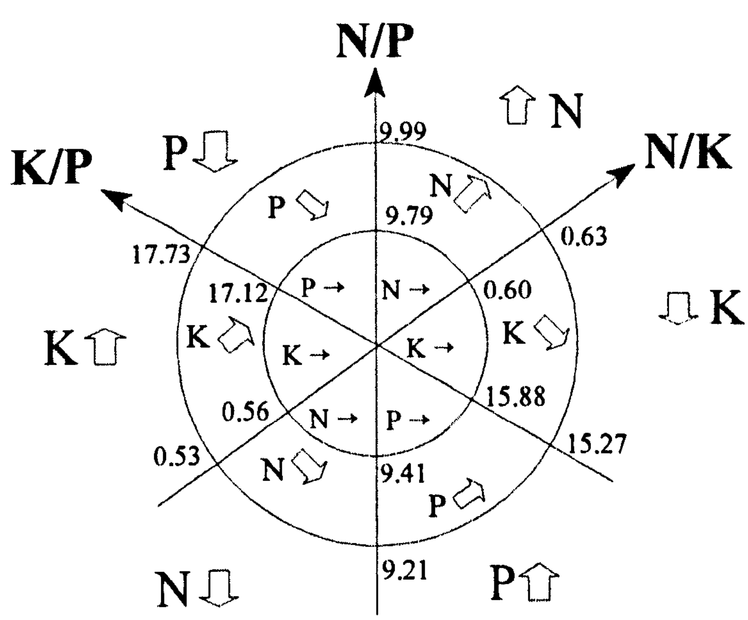

Figure 6.7. DRIS interpretation chart for nutrient ratios calculated from nutrient concentrations within whole potato plant dry matter, at 56 DAP in an investigation of the growth and yield response to basal, tuber initiation and supplementary foliar N of potatoes infected by potato cyst nematodes.

Table 6.11. DRIS chart and indices interpretation for nutrient ratios calculated from nutrient concentrations within whole plants at 56 DAP in an investigation of the growth and yield response to basal, tuber initiation and supplementary foliar N of potatoes infected by potato cyst nematodes.

treatment	Chart[a]	In[b]	Ip[c]	Ik[d]	Ranking[e]	tuber yield (t/ha)
NORM+O[f]	norm data	0	0	0	N = P = K	51.6
NORM	P↓ K↘ N→	49	-55	6	P > K > N	25.7
NORM+F	P↓ K↓ N→	55	-58	3	P > K > N	29.1
HIGH+F	P↓ K↓ N→	63	-70	6	P > K > N	24.5
ALL+F	P↓ K↓ N→	50	-49	-1	P > K > N	22.9

[a] nutrient balance derived from the DRIS chart; [b] nitrogen index; [c] phosphate index; [d] potassium index; [e] order of nutrient requirement; [f] for treatments see Table 4.3

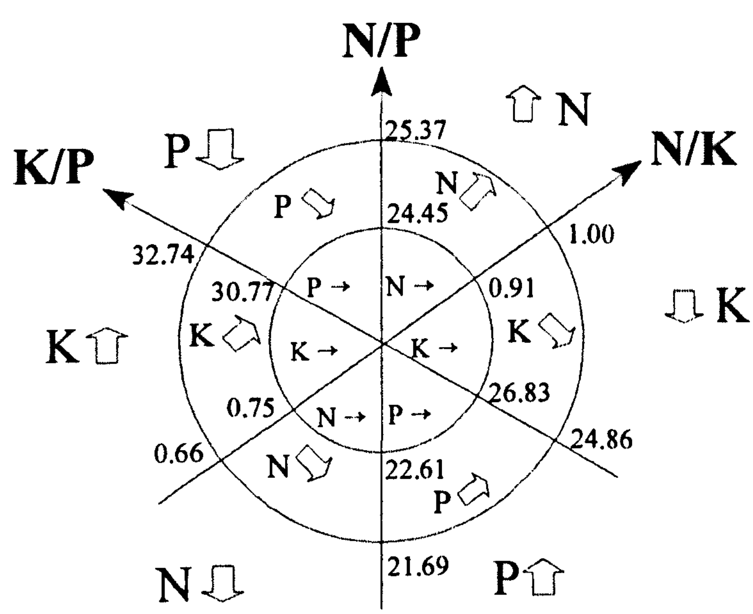

Figure 6.8. DRIS interpretation chart for nutrient ratios calculated from nutrient concentrations within potato fourth leaf plus petiole at 107 DAP in an investigation of the growth and yield response to basal, tuber initiation and supplementary foliar N of potatoes infected by potato cyst nematodes.

Table 6.12. DRIS chart and indices interpretation for nutrient ratios calculated from nutrient concentrations within the fourth leaf plus petiole at 107 DAP in an investigation of the growth and yield response to basal, tuber initiation and supplementary foliar N of potatoes infected by potato cyst nematodes.

treatment	Chart[a]	In[b]	Ip[c]	Ik[d]	Ranking[e]	tuber yield (t/ha)
NORM+O [f]	N→ P→ K→	0	0	0	N = P = K	51.6
NORM	N↘ K↘ P→	-3	8	-5	K > N > P	25.7
NORM+F	K↘ N→ P→	6	1	-7	K > P > N	29.1
HIGH+F	N→ P→ K→	6	0	-6	K > P > N	24.5
ALL+F	P↓ N→ K→	15	-18	3	P > K > N	22.9

[a] nutrient balance derived from the DRIS chart; [b] nitrogen index; [c] phosphate index; [d] potassium index; [e] order of nutrient requirement; [f] for treatments see Table 4.3

6.3.6 Field experiment 1998

The growth and yield response of field grown potatoes to supplementary broadcast granular or foliar applied phosphate when infected by potato cyst nematodes.

The treatment chosen as most representative of a high yielding (norm) plant population was the standard fertiliser application in plots treated with oxamyl. At 30 and 57 DAP, nutrient ratios were calculated from nutrient concentrations within the dry matter of whole plants (Table 6.13). The DRIS chart (Figure 6.9 and Table 6.14) at 30 DAP suggested that, in plots not treated with oxamyl, the standard P application (100 kg P_2O_5/ha) resulted in nutrient balance; increasing the broadcast granular application to 110.2 kg P_2O_5/ha resulted in a moderate K limitation; increasing the broadcast granular application to 120.4 kg P_2O_5/ha resulted in nutrient balance; applying 10.2 kg P_2O_5/ha or 20.4 kg P_2O_5/ha as foliar P resulted in moderate K limitation. DRIS indices (Table 6.14) suggested that, in all plants from plots not treated with oxamyl, the most limiting nutrients were K followed by N.

DRIS chart interpretation of nutrient ratios at 57 DAP (Figure 6.10 and Table 6.15) suggested that, in plots not treated with oxamyl the standard P application (100 kg P_2O_5/ha) resulted in nutrient balance; increasing the broadcast granular application to 110.2 P_2O_5/ha resulted in a moderate K limitation and increasing it to kg 120.4 kg P_2O_5/ha resulted in moderate P and K limitation. Applying foliar P at 10.2 kg P_2O_5/ha resulted in a P limitation, whereas applying it at 20.4 kg P_2O_5/ha resulted in nutrient balance. The DRIS indices (Table 6.15) further suggested that K limitation also existed in both the broadcast granular applications of 120.4 kg P_2O_5/ha and the Std (control). Plants shown to have severe P or K limitations produced substantially lower tuber yields (Table 6.15). Simple linear regression suggested no relationship between the ratios of N/P, N/K or K/P and final tuber yield.

Table 6.13. Nutrient ratios calculated from nutrient concentrations within whole plant dry matter at 30 and 57 DAP in a field investigation of the growth and yield response to supplementary broadcast granular and foliar P of potatoes infected by potato cyst nematodes.

	30 DAP			57 DAP		
treatment	N/P	N/K	K/P	N/P	N/K	K/P
Std +O [a]	7.03	0.58	12.20	6.90	0.50	13.90
Std	6.98	0.60	11.85	7.31	0.53	13.92
Std + BP1	6.98	0.63	11.14	7.69	0.56	13.64
Std + BP2	7.00	0.60	11.71	7.32	0.51	14.42
Std + FP1	6.80	0.59	11.56	7.14	0.49	15.22
Std + FP2	6.96	0.61	11.37	6.91	0.51	13.52

[a] for treatments see Table 5.1.

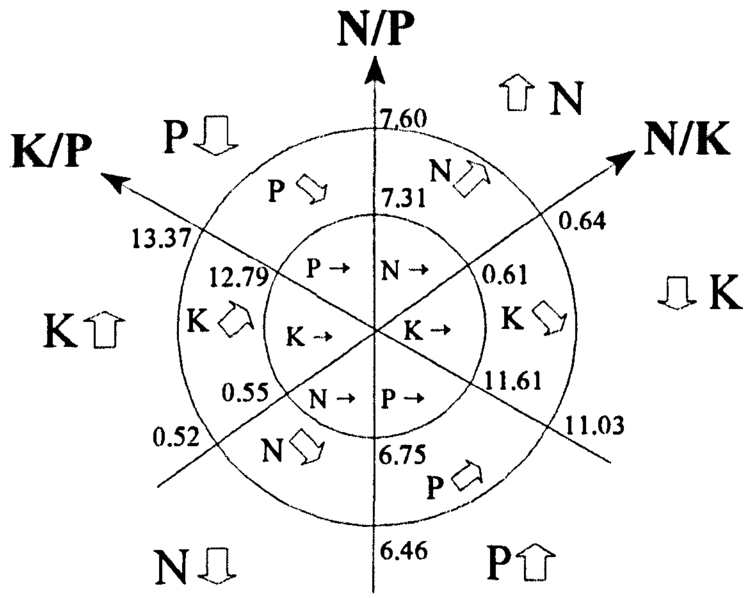

Figure 6.9. DRIS interpretation chart for nutrient ratios from whole potato plant dry matter at 30 DAP in a field investigation of the growth and yield response to supplementary broadcast granular and foliar P of potatoes infected by potato cyst nematodes.

Table 6.14. DRIS chart and indices interpretation for nutrient ratios calculated from nutrient concentrations within whole plant dry matter at 30 DAP in a field investigation of the growth and yield response to supplementary broadcast granular and foliar P of potatoes infected by potato cyst nematodes.

treatment	Chart[a]	In[b]	Ip[c]	Ik[d]	Ranking[e]	tuber yield (t/ha)
Std +O [a]	N→ P→ K→	0	0	0	N = P = K	58.7
Std	N→ P→ K→	2	3	-5	K > N > P	50.6
Std + BP1	K↘ N→ P→	5	7	-12	K > N > P	47.1
Std + BP2	N→ P→ K→	2	3	-5	K > N > P	48.4
Std + FP1	K↘ N→ P→	-2	7	-5	K > N > P	49.3
Std + FP2	K↘ N→ P→	3	6	-9	K > N > P	45.1

[a] nutrient balance derived from the DRIS chart; [b] nitrogen index; [c] phosphate index; [d] potassium index; [e] order of nutrient requirement; [f] for treatments see Table 5.1

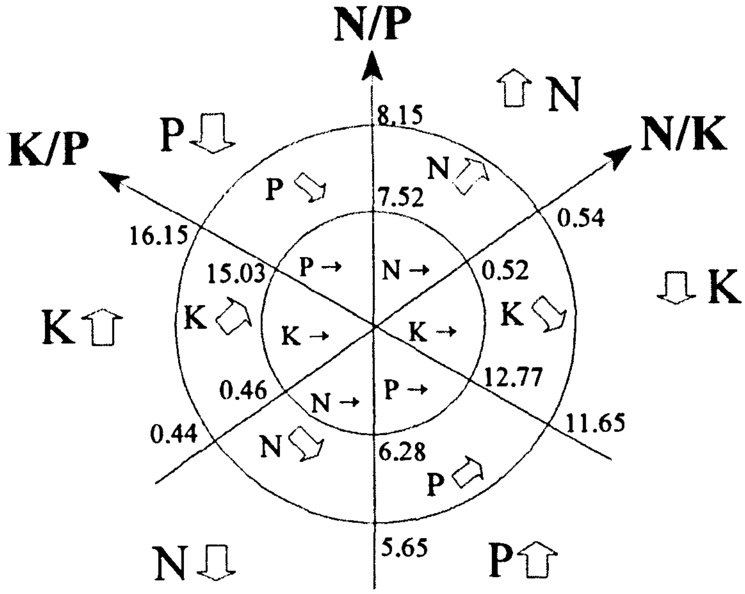

Figure 6.10. DRIS interpretation chart for nutrient ratios calculated from nutrient concentrations within whole potato plant dry matter at 57 DAP in a field investigation of the growth and yield response to supplementary broadcast granular and foliar P of potatoes infected by potato cyst nematodes.

Table 6.15. DRIS chart and indices interpretation of nutrient ratios calculated from nutrient concentrations of whole plant dry matter at 57 DAP in a field investigation of the growth and yield response to supplementary broadcast granular and foliar P of potatoes infected by potato cyst nematodes.

treatment	Chart[a]	In[b]	Ip[c]	Ik[d]	Ranking[e]	tuber yield (t/ha)
Std +O [f]	N→ P→ K→	0	0	0	N = P = K	58.37
Std	N→ P→ K→	6	-2	-4	K > P > N	50.6
Std + BP1	K↘ N→ P→	12	-3	-9	K > P > N	47.1
Std + BP2	P↘ K↘ N→	4	-4	0	P > K > N	48.4
Std + FP1	P↘ N→ K→	0	-5	5	P > N > K	49.3
Std + FP2	N→ P→ K→	1	2	-3	K > N > P	45.1

[a] nutrient balance derived from the DRIS chart; [b] nitrogen index; [c] phosphate index; [d] potassium index; [e] order of nutrient requirement; [f] for treatments see Table 5.1

6.3.7 Glasshouse experiment 1998

The treatment chosen as most representative of a high yielding (norm) plant population was the standard fertiliser application in plots treated with oxamyl. At 47 DAP, nutrient ratios were calculated from nutrient concentrations within the dry matter of whole plants (Table 6.16). DRIS chart interpretation (Figure 6.11 and Table 6.17) of nutrient ratios at 47 DAP suggested that, in plots not treated with oxamyl, only the supplementary application of 20.4 kg P_2O_5/ha as foliar P resulted in moderate K limitation. DRIS indices (Table 6.19) showed that, in plots not treated with oxamyl, the standard P application (100 kg P_2O_5/ha) resulted in an N limitation; increasing the broadcast granular application to either 110.2 P_2O_5/ha or 120.4 kg P_2O_5/ha resulted in a P followed by a K limitation; applying 10.2 kg P_2O_5/ha or 20.4 kg P_2O_5/ha as foliar phosphate resulted in a K followed by N limitation. The effect of applying additional phosphate to plots appears to be dependent on the method of application; applying additional phosphate in the broadcast granular form results in P limitation whereas applying additional phosphate in the foliar form results in a K limitation.

Table 6.16. Nutrient ratios calculated from nutrient concentrations within whole plant dry matter at 47 DAP in a glasshouse investigation of the growth and yield response to supplementary broadcast granular and foliar P of potatoes infected by potato cyst nematodes.

treatment	N/P	N/K	K/P
Std +O [a]	6.53	0.48	13.81
Std	6.33	0.45	13.99
Std + BP1	7.02	0.50	13.98
Std + BP2	6.96	0.51	13.78
Std + FP1	6.49	0.51	12.87
Std + FP2	6.05	0.51	11.87

[a] for treatments see Table 5.1.

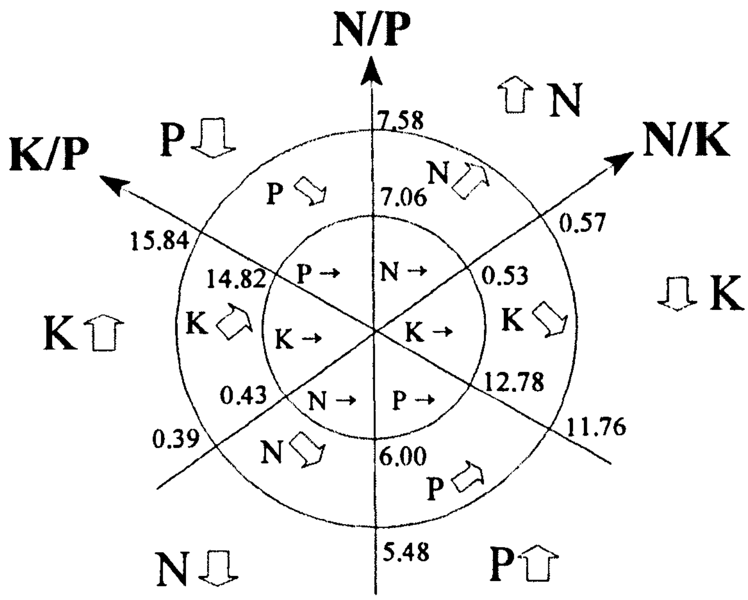

Figure 6.11. DRIS interpretation chart for nutrient ratios calculated from nutrient concentrations within whole plant dry matter at 47 DAP in a glasshouse investigation of the growth and yield response to supplementary broadcast granular and foliar P of potatoes infected by potato cyst nematodes.

Table 6.17. DRIS chart interpretation and nutrient indices for the nutrient ratios calculated from nutrient concentrations within whole plant dry matter at 47 DAP in a glasshouse investigation of the growth and yield response to supplementary broadcast granular and foliar P of potatoes infected by potato cyst nematodes.

treatment	Chart[a]	In[b]	Ip[c]	Ik[d]	Ranking[e]
Std +O [f]	N→ P→ K→	0	0	0	N = P = K
Std	N→ P→ K→	-4	1	3	N > P > K
Std + BP1	N→ P→ K→	5	-4	-1	P > K > N
Std + BP2	N→ P→ K→	5	-3	-2	P > K > N
Std + FP1	N→ P→ K→	2	4	-6	K > N > P
Std + FP2	K↘ N→ P→	-1	11	-10	K > N > P

[a] nutrient balance derived from the DRIS chart; [b] nitrogen index; [c] phosphate index; [d] potassium index; [e] order of nutrient requirement; [f] for treatments see Table 5.1

6.4 Discussion

6.4.1 Experiment one 1996

The effects of fertiliser application type and foliar NPK on the growth and yield response of potatoes infected by the potato cyst nematode, *G. pallida*.

Where all of the fertiliser was applied pre-planting as a broadcast granular application the order of limiting nutrients was determined as K > P > N and this equates well to the nutrient concentrations reported in section 3.3.4. Where the fertiliser was split between broadcast granular and foliar NPK applications, however, the order of nutrient limitation to crop growth was calculated as N = K > P. As the K and P concentrations were both increased as a result of the foliar application but the N concentration was not, it is clear why the change from a P limitation to an N limitation occurred. The nutrient concentration within plants from these plots were similar to the concentrations within plants from oxamyl treated plots so no deficiency would be shown by conventional comparisons. Where the fertiliser was applied as all liquid placed or split between liquid placed and foliar NPK, the nutrient requirement of plants from plots not treated with oxamyl was in the order of N > K > P. This would directly contradict the interpretation of the nutrient concentrations (section 3.3.4), which show N, P and K concentrations within plants from plots not treated with oxamyl as much higher than those within plants from oxamyl treated plots. As the tuber yields from the liquid placed fertiliser plots were similar to those from oxamyl treated plots no nutrient disorders would be expected. However, liquid placement of fertilisers has been shown to increase the uptake of applied nutrients (Lewis, 1994), so the resulting higher nutrient concentrations would appear as a nutrient imbalance when compared to the concentrations arising from broadcast granular applications. When the N, P and K concentrations were compared to the published sufficiency ranges (Walworth & Muniz, 1993), only the plants from plots receiving no fertiliser showed substantially lower N concentrations, all plants contained higher levels of P, and all plants contained substantially lower concentrations of K. This underlines the potential of nutrient ratios to identify nutrient limitations where their concentrations are higher than those found in control plants.

6.4.2 Experiment two 1996

The effects of individual and combined applications of foliar N PK on the growth and yield response of potatoes infected by the potato cyst nematode *G. pallida*

Without exception, all nutrient ratios calculated for plants from plots not treated with oxamyl suggest that P was the most limiting nutrient. This compares well to the nutrient concentrations (section 3.4.4) as P was shown to be reduced in plants from plots not treated with oxamyl. The statistical analysis of the nutrient concentrations, however, did not suggest any deficiencies and also showed that N, P and K concentrations were reduced to a similar degree. When the nutrient concentrations were compared to the published sufficiency ranges, all plants contained higher P concentrations but lower N and K concentrations than those classed as sufficient by Walworth & Muniz (1993). However, difficulties were encountered in making these comparisons because the sampling times were different. Where the nutrient concentrations changed dramatically between sampling times in the literature, selecting an earlier or later time gave either a deficiency or an excess of any chosen nutrient. As two of the five foliar nutrient applications had been made at the time of sampling, applications of foliar P would be expected to ameliorate the perceived deficit shown by the nutrient ratios. However, the strength of the P limitation for the foliar P treatment (ratio index -13) suggests that this was not the case and, in addition, the actual P concentration was one of the lowest recorded. Therefore, it is possible that the foliar applied P had not been absorbed into the leaf, although this would oppose the controlled environment findings of Lewis & Kettlewell (1993), who showed that Pentland Dell potato plants readily absorbed foliar P. In fieldwork by Lewis

(1994), however, several cases are reported where foliar P applications gave reduced P concentration within plant dry matter. In addition, comparative work on plant response to the application of foliar P to glasshouse and field grown plants, shown in this thesis, also suggests that glasshouse grown plants readily absorb foliar P whilst the response of field grown plants is variable. There is evidence to suggest, therefore, that the foliar P applied in this experiment may not have been absorbed and, consequently, could do nothing to redress the P limitation which existed within the plants. The final yield of plants from plots receiving foliar P (38.7 t/ha) also suggests that the P deficit could be responsible for the yield reduction. However, applications of foliar N and K gave a similar P nutrient ratio index (-15) but produced a yield of 43.8 t/ha, which was slightly higher than in the control plots treated with oxamyl.

6.4.3 Experiment one 1997

The growth and yield responses to supplementary foliar nitrogen and foliar phosphate of potatoes infected by potato cyst nematodes

At 61 DAP, before the application of any foliar nutrients to plants in plots not treated with oxamyl, all nutrient ratios rank the order of nutrient requirement as P > K > N, with a severe P limitation. These results support the findings of significantly lower ($P < 0.001$) N, P and K concentrations measured in all plants from plots not treated with oxamyl (section 4.3.4). However, without the ratios, selecting which nutrient was most limiting would be difficult. Equally, the identification of a limiting nutrient from published deficiency and sufficiency ranges would also be speculative. The nutrient concentrations at 61 DAP were 3.16 %N, 0.243 %P and 5.40 %K which, compared to the published sufficiency concentrations of Walworth & Muniz (1993) of 3.9 %N and 0.24 %P at 67 DAP, and 2.14 %K at 60 DAP or 6.49 % at 70 DAP, would suggest that the most limiting nutrients were N and possibly K.

When compared to the more general sufficiency ranges given by Bennett (1993) of 2.0 to 5.0 %N, 0.2 to 0.5 %P and 1.0 to 5.0 %K the only imbalance would be an excess of K. It is suggested by Bennett (1993), however, that the imbalance caused by any excess of a non-toxic nutrient, e.g. K, may detrimentally affect plant growth. Therefore, although statistical analysis shows that N, P and K concentrations were all significantly reduced, the use of nutrient ratios removes the ambiguity of which nutrient is most limiting. However, whereas the nutrient ratios agree in part with Bennett (1993), that an imbalance could be causing reduced plant growth, they oppose the P sufficiency and N limitation suggested by comparison with the values given by Walworth & Muniz (1993). Consequently, as all of the heavily-infected plants produced substantially lower plant fresh-weights and final tuber yields than the lightly-infected plants, it is debatable as to whether P or N limitation was responsible.

Leaf samples were taken at 104 DAP, which was after two of the four foliar nutrient applications of the four spray programme and three applications of the five spray programme. The calculated ratios for all plants heavily-infected by PCN suggest that K was severely limiting plant growth. The nutrients P and N were shown by the indices to be greatly in excess, but as remedial actions cannot remove nutrients from the plants, it is only possible to re-balance the nutrients by adding additional K. These results agree in part with the nutrient concentrations (section 4.3.4), which showed that heavily-infected plants contained significantly (P <0.001) more N and P than lightly-infected plants. However, the K concentrations were similar in lightly- and heavily-infected plants, which would suggest that K was not affecting crop growth. Nevertheless, by accounting for the balance of nutrients within the plant, the nutrient ratios suggests a potential yield limitation arising from this K concentration. When the mean nutrient concentrations from heavily-infected plants (3.84 %N, 0.155 %P, 4.67 %K) were compared with the published sufficiency ranges, several conclusions could be drawn. Walworth & Muniz (1993) suggest that, for whole leaves, 3.0 to 4.0 %N, 0.25 to 0.40 %P and 6.0 to 8.0 %K would be adequate for unrestricted growth when tubers were half grown, which would suggest that both P and K were limiting in my experiment. Piggott (1986), however, suggests that for the youngest mature blade plus petiole 3.0 to 5.0 %N, 0.1 to 0.3 %P and 4.0 to 8.0 %K are sufficient for plant growth when tubers are half grown. These latter values do offer a better comparison as the same plant parts were used in the 104 DAP sample, but no deficiency or excess would be suggested. Therefore, of the three interpretation methods, the statistical analysis suggests N and P excess; the sufficiency values given by Piggott (1986) suggest no nutrient deficiency; whereas those of Walworth & Muniz (1993) suggest P and K deficiencies, even from the very high yielding oxamyl plots; and the nutrient ratios suggest a severe K deficiency brought about by excess of N and P. However, as any additional P applications to ameliorate the deficiency suggested by the values of Walworth & Muniz (1993) are likely to further intensify the nutrient imbalance, only the nutrient ratios which identify K as most limiting, would appear to offer a feasible remedial solution. As all plants heavily-infected by PCN produced substantially reduced tuber yields, a distinct K limitation during the latter part of the growing season could be compounding the earlier P or N limitation, thus further reducing plant growth and yield.

6.4.4 Experiment two 1997

The growth and yield responses to supplementary foliar nitrogen of potatoes infected by potato cyst nematodes

Plant sampling was carried out prior to the application of foliar nutrients at 58 DAP. As with the previous experiment, nutrient ratios again suggest that the order of nutrient requirement was P > K > N, with P severely limiting plant growth. These results again support findings of significantly lower ($P < 0.003$) N, P and K concentrations measured in all plants heavily-infected by PCN (section 4.4.4). The range of concentrations found in the whole plant dry matter were similar to those in the previous experiment and comparisons with published values, therefore, highlight the same potential limitations of N and K. Leaf samples taken at 98 DAP were only analysed for %N, as required by the experiment design, so no nutrient ratios could be calculated for this later timing. However, as all of the plants heavily-infected by PCN produced substantially lower yields than to lightly-infected plants, a nutrient limitation may have been responsible for the reduced plant growth. The application of 4% and 6% foliar N did improve yields (by approximately 4t/ha) and, therefore, although N was identified by nutrient ratios as the least limiting nutrient, the foliar N applications were beneficial. This could confirm that the N and K limitation, identified by comparison with sufficiency values of Walworth & Muniz (1993), were indeed the nutrients limiting crop growth and tuber yield. These findings would also then agree with those from the 1996 experiment with individual and combined applications of foliar N, P and K, where foliar N and K applications gave a yield slightly above that of the oxamyl treated control. This may also confirm why the application of early foliar P followed by foliar N, in the 1997 foliar P and foliar N experiment, produced no yield benefit even though the suggested order of nutrient requirement from nutrient ratios were P > K > N. It is also worthy of note that where foliar P and K were applied in the 1996 experiment with individual and combined applications of foliar N, P and K, no yield improvement was seen. Consequently, it is suggested that, as no foliar nutrient applications were made with benefit of nutrient ratio analysis, the final tuber yields suggest that nutrient sufficiency ranges of Walworth & Muniz (1993) for plants at 67 DAP had highlighted the correct order of nutrient limitation. However, it must be stressed that N and K concentrations within lightly-infected plants would also be classed as deficient according to Walworth & Muniz (1993), yet the yields from these plants were in excess of 50 t/ha.

6.4.5 Experiment three 1997

The growth and yield responses to basal, tuber initiation and supplementary foliar nitrogen of potatoes infected by potato cyst nematodes

Whole plant samples were taken at 56 DAP. As with the previous two experiments, a severe P limitation was suggested by the nutrient ratios, with the order of nutrient requirement P > K > N. These results agree with the significant ($P < 0.001$) reduction of N, P and K concentrations measured in heavily-infected plants. A point of particular interest here, is that when all of the fertiliser N was applied to the seedbed at planting, the N, P and K concentrations within plants from these plots were increased. However, these increased nutrient concentrations did not alter the ratio of nutrients and P remained the most limiting. Comparisons with the published sufficiency values of Walworth & Muniz (1993) for plants at 50 DAP suggest that both N and P concentrations were substantially lower or, in plants at 67 DAP, were similar for %N but substantially higher for %P, for all plants within the experiment. This type of comparison again highlights the difficulties of making accurate nutrient disorder diagnosis from published values and no real conclusions could be drawn from them. Nevertheless, all heavily-infected plants produced a substantially lower yield than those only lightly-infected and, therefore, the P limitation, denoted by the nutrient ratios could be causal.

The nutrient ratios obtained from leaf samples taken at 107 DAP added further weight to the evidence that K was limiting within heavily-infected plants in the latter part of the season. The most limiting nutrient within plants from plots which had received all of the N at planting and supplementary foliar N, however, was suggested to be P by the nutrient ratios. This would not be entirely unexpected as the anion uptake of plants supplied with NO_3^- - N greatly exceeds their cation uptake, which increases rhizosphere pH and leads to a reduced uptake of P (Mengel & Kirkby, 1987). The nutrient ratios also highlighted that the Std (control) plants placed the nutrient requirement order as K > N > P but, when foliar N was also applied, the nutrient requirements changed to K > P > N. It would appear, therefore, that the five applications of 4% foliar N had rectified the N limitation. In contrast to this, the statistical comparisons show that the concentrations of N and P were significantly ($P < 0.05$) higher within the Std (control) plants whilst the K concentration was unaffected, suggesting that no nutrient deficiency existed. Comparisons with published values, however, generally suggest that a P deficiency existed (Piggott, 1993), or that K was approaching deficiency (Walworth & Muniz, 1993). It is again worthy of note, nonetheless, that the deficiencies suggested by published values would also include plants from plots treated with oxamyl, which were very high yielding and would not be limited by nutrient deficiency.

6.4.6 Field experiment 1998

The growth and yield response of field grown potatoes to supplementary broadcast granular or foliar applied phosphate when infected by potato cyst nematodes

The delayed plant emergence resulting from root invasion by PCN in the 1997 experiment was hypothesised to be the result of reduced nutrient uptake during pre- or early post-emergence plant growth. The nutrient concentrations measured at 30 DAP show significantly lower concentrations of N and K within heavily-infected plants but no effect on the P concentration. Nutrient ratios confirm that these potential deficiencies existed in all heavily-infected plants and place the order of nutrient requirement as K > N > P. No published values for nutrient concentrations at this early growth stage could be found and, therefore, no comparisons are possible. The nutrient ratios do, nonetheless, offer a further nutrient diagnostic method which aids the interpretation of statistical results. The ratios also confirm that applying supplementary broadcast granular P did not affect the nutrition of the plant and dispute the requirement for additional P at this growth stage.

When whole plant samples were taken at 57 DAP, plants from the Std (control), Std + BP1 and Std + FP2 were shown by the nutrient ratios to be limited by K. Plants from the Std + BP2 and Std + FP1 plots, in contrast, were shown to be limited by P. This is despite the statistical analysis not showing any significant reductions of N, P or K concentrations within plants heavily-infected by PCN, although P and K concentrations were lower than within lightly-infected plants. This outlines one of the differences between statistical evidence and ratio comparison, as the statistical analysis would require significance for the evidence to be meaningful. The mean concentrations for the heavily infected plants were 3.65 %N, 0.503 %P and 7.07 %K and, compared to published sufficiency concentrations of Walworth & Muniz (1993) of 3.9 %N and 0.24 %P at 67 DAP, and 2.14 %K at 60 DAP, N could be suggested to be low with P and K in great excess, although the sampling time for N and P does not really justify the comparison. When compared to the more general sufficiency ranges given by Bennett (1993) of 2.0 to 5.0 %N, 0.2 to 0.5 %P and 1.0 to 5.0 %K, only K would be suggested as potentially in excess. This again highlights the problems of finding comparable published values for nutrients within literature and is why Gascho *et. al.* (1993) favours nutrient ratios as a diagnostic tool. Where the reduced yields were seen from heavily-infected plants, therefore, this could have arisen either as a result of a reduced N concentration, in line with Walworth & Muniz (1993), or by an imbalance of P or K as denoted by the nutrient ratios.

6.4.7 Glasshouse experiment 1998

The growth response of glasshouse grown potatoes to supplementary broadcast granular or foliar applied phosphate when infected by potato cyst nematodes

Whole plant samples were taken at 47 DAP. N, P and K concentrations were not shown to be significantly different between plants from pots treated or not treated with oxamyl (section

5.4.3). Nutrient ratios, however, show an N limitation within the Std (control) plants, P limitation within plants receiving supplementary broadcast granular P, and a K limitation within plants receiving supplementary foliar P. Applying supplementary P as a foliar treatment significantly ($P = 0.004$) increased the plant P concentration above that seen in plants which had received supplementary P as a broadcast granular. It is not surprising, therefore, that the nutrient ratios change from a P limitation with the broadcast application to a K limitation with the foliar application. Consequently, using the nutrient ratios provides a more detailed view of the nutrient requirements of the plant than statistical analysis. When compared to Bennett's (1993) sufficiency ranges, all of the nutrient concentrations suggest adequate N concentrations but excessive quantities of P and K. The sufficiency values from Walworth & Muniz (1993), however, would suggest very low N concentrations, adequate P concentrations but no comparable values for K. However, although plants from the supplementary foliar P application showed no P limitation, the plants receiving supplementary broadcast granular P showed no benefit to the total plant fresh-weights and leaf area (section 5.4.2) were seen. This could suggest, therefore, that if the foliar applications had been based on the ratio analysis of the Std (control) plants (which suggest an N limitation) as opposed to pre-determined P applications, the correct remedial applications could have given plant growth benefits. Although the root invasion analysis shows that no differences existed between plants from oxamyl treated and untreated pots, the growth analysis suggested that some benefit had been derived from the oxamyl application. Nutrient ratios would, therefore, be valid in these comparisons.

6.5 Conclusions

The identification of nutrient deficiencies using conventional techniques was shown to be problematical where comparisons to published sufficiency ranges were made and often inconclusive using statistical analysis. The use of nutrient ratios not only overcame these problems but also provided information of the nutrient requirement order. Furthermore, where the nutrients investigated were shown to be sufficient or in excess, the nutrient ratios still identified the imbalance and specified nutrients potentially limiting crop growth. In six out of the eight field experiments it is suggested that P was the most limiting and K the second most limiting nutrient within PCN-infected plants up to 82 DAP. In the remaining two field experiments K was suggested to be the most limiting and P the second most limiting nutrient within PCN-infected plants up to 82 DAP. Where nutrient samples were taken later in the season K was suggested as the most limiting nutrient. However, as no real relationships could be shown between the nutrient ratios and the final tuber yields, these results should be treated with caution. The nutrient ratios were not, however, used to determine which nutrients were applied and, therefore, no evidence was gained to suggest that remedial applications, based on ratio diagnosis, would not have benefited crop growth. In addition, as the ability of nutrient ratios to highlight nutrient disorders is increased by inclusion of as many nutrients as possible, a more comprehensive investigation may clarify the usefulness of nutrient ratios as a diagnostic tool for nematode infected plants.

7. General discussion and conclusions

7.1 General discussion

The main aims of this research were to investigate whether foliar applied nutrients could ameliorate nutrient deficiencies associated with PCN infection of potatoes, thus increasing the tuber yield and PCN tolerance of infected potato plants. However, as the basal seedbed fertiliser would provide nutrients to the pre- and early post-emergent plant, it was necessary to determine whether the method of basal fertiliser application would also influence the plant's PCN tolerance.

7.1.1 The effects of fertiliser application method on plant PCN tolerance

The two methods of seedbed fertiliser application investigated in this research were the broadcasting of granular fertilisers and the placement of liquid fertilisers. Neither of these two methods of fertiliser application significantly affected the final PCN population densities, the numbers of juveniles counted in the roots, the speed of plant emergence, percentage ground cover, total tuber yield or tolerance of the plants. Nonetheless, placed liquid fertilisers gave small benefits to the percentage ground cover, plant fresh-weight and final tuber yield and some improvement of the nutrient status of the plants in plots not treated with oxamyl. The small yield increases were a consequence of greater ground cover as crop canopy size and tuber yield are positively correlated (Gunasena, 1969; Millard & Marshall, 1986), however, yield increases can only occur in response to physiological changes within the plants. Therefore, as the placed liquid fertiliser increased the N, P and K concentrations within plants, the improved plant nutrient status may have been beneficial to plant growth. Correct placing of liquid (or granular) fertilisers increases the nutrient concentrations of plants by putting the nutrients in closer proximity to the roots, whereas broadcast fertilisers distribute the nutrients throughout the cultivated layer of the soil (Lewis, 1994). The improved efficiency of placed fertiliser (Baerug & Steenbury, 1971) with respect to P can arise from reduced P adsorption onto the soil (Knittel, 1988). This was demonstrated where 'placing' only 40 kg P_2O_5/ha produced equivalent tuber yields to broadcast granular applications of 60 to 120 kg P_2O_5/ha (Cooke, 1949). However, although there was some evidence to suggest that placing liquid fertilisers improved the nutrient status of the PCN-infected plants in my research, no significant benefits to tuber yields, and therefore PCN tolerance of plants, were seen over those achieved by broadcasting granular fertilisers. The method of seedbed fertiliser application, therefore, could not be classed as critical to the plants' tolerance of PCN attack and was not a major consideration in the design of the later experiments which investigated the use of foliar applied nutrients and the tolerance of PCN-infected plants. In addition to the seedbed fertiliser application method, foliar applications of N, P and K, which replaced 33% of the seedbed applied fertilisers, investigated the potential for foliar fertilisers to by-pass the PCN-damaged root system, ameliorate PCN-induced nutrient deficits, and thus improve the plant tolerance of PCN attack. The results show that, although foliar applications resulted in no additional plant growth or yield increases above those where seedbed fertiliser was used alone, there were no detrimental effects of applying the fertiliser by the foliar route. This suggests, therefore, that foliar applications can effectively replace the seedbed fertiliser applications for plants infected by PCN. However, foliar applications did increase the N, P and K concentrations within the plants and these increases were proportionally greater when foliar nutrient applications were made to plots also receiving liquid placed seedbed fertiliser. Although foliar nutrients are readily absorbed by foliage (Gray, 1977; Barel & Black, 1979a), it is unlikely that they were the sole cause of the increased plant nutrient concentrations, which may also have resulted from increased nutrient uptake by the roots, stimulated by foliar nutrient application (Thorne, 1957). Thus, the greater efficiency and availability of fertiliser nutrients from the liquid placed application method (Baerug & Steenbury, 1971) may have provided a more easily exploited nutrient source for the additional root nutrient uptake and, therefore, have led to the higher plant nutrient concentrations. In addition, although the foliar N, P and K applications to plants in liquid fertiliser plots produced the highest plant N, P and K concentrations, the tuber yield and PCN-tolerance of these plants were no greater than that of plants receiving foliar N, P and K from broadcast granular fertiliser. It is worthy of note, however, that the experiment was carried out on soils with a low initial PCN population density; further work would be required to determine whether foliar N, P and K applications with liquid placed fertilisers would be of equal or greater benefit to plant PCN tolerance at greater PCN soil infestations.

7.1.2 Timing of broadcast granular N applications

Where root systems are struggling to develop under PCN attack, Trudgill (1980) suggested that the lower growth rates of PCN-infected plants could be due to a reduced uptake of N and P. It was hypothesised that 'benefits to the growth of PCN-infected plants may occur if all of the recommended quantity of N was applied at planting', giving a greater availability of N to the damaged roots during early crop growth and, thus, increased plant growth. Nitrogen applications were split between planting and tuber initiation at 50/50, 66/33 and 100/0% of the recommended N quantity. In addition, all of the N application regimes, except for the 50/50 split in the Std (control), received five 4% supplementary foliar N applications to investigate further the tolerance benefits seen from this treatment in the foliar N, P and K experiment in 1996. Plant nutrient analysis at 56 DAP showed that increasing the N quantity applied at planting significantly increased the N concentration within PCN-infected plants. However, these concentrations were still significantly lower than those of the lightly-infected plants from oxamyl treated plots and, as no benefits to early plant growth were seen, suggest that N may still have been limiting plant growth eight weeks after planting, as suggested by Trudgill *et al.*

(1975a). Plant nutrient analysis at 107 DAP showed that when all of the N was applied at planting the lowest N and P concentrations occurred. The reduced N concentration was probably caused by loss of fertiliser N through leaching (Gunasena, 1969; Gunasena & Harris, 1971), which subsequently reduced P uptake due to the synergistic interaction of these two nutrients (Lewis, 1986). Furthermore, as the N application at planting increased from 50 to 66 and then to 100%, the percentage ground cover after 104 DAP diminished more rapidly and, probably as a consequence of this, tuber yields were reduced. When five supplementary 4% foliar N applications were made in addition to the 50/50 split of planting and tuber initiation N, however, small ground cover improvements throughout the season probably caused the tuber yield and tolerance improvements. This suggests that some benefits were derived from the supplementary N applications, which supports the suggestions of Haverkort *et al.* (1994) that N may be limiting in the latter part of the season. However, as the heavily-infected plants produced poor early season ground cover, which coincides with the most influential period of incident radiation for the growth of second early and maincrop potatoes in the UK (Allen & Scott, 1992), no major ground cover or yield increases could be expected from foliar N applications which started during tuber initiation, and thus after plant size had influenced the potential for further leaf growth (Allen & Scott, 1980).

7.1.3 Application timing and quantity of foliar N, P and K

In the 1996 experiments, foliar N, P and K applied singly or in combined applications, showed the potential of both foliar N and foliar N + K applications to improve plant growth, tuber yield and tolerance of PCN-infected plants. However, although foliar N applications improved the N concentrations within PCN-infected plants, the foliar N + K applications did not redress the PCN-induced N and K deficits shown within the Std (control) plants. Therefore, it appears that the plant growth improvements from foliar N + K applications did not arise from improved plant nutrient status. The application of foliar N and foliar N + K, however, greatly increased the leaf area index at 110 DAP, which would have given higher tuber yields (MacKerron & Waister, 1985). Furthermore, foliar N applications increased the number of tubers and yield in the 40-60 mm grade, whilst foliar N + K applications gave increased tuber numbers and yield in both the < 40 and 40-60 mm grades. Consequently, the foliar N application alone would be of more benefit to commercial growers as only the quantity of tubers in the saleable grade was increased with this treatment. In addition, although the foliar nutrients were supplementary to the recommended quantities, where they were made to plants in oxamyl treated plots the yield was unaffected by foliar N + K applications and only slightly increased by foliar N applications, suggesting that supplementary nutrients had not affected their yield.

Applying foliar N at three rates (2, 4 and 6%) again demonstrated the small ground cover and yield benefits from five 4% foliar N applications. Increasing the application quantity to 6% N gave a small additional yield increase but decreasing the foliar application to 2% N gave a tuber yield as low as that of the Std (control) treatment, which received only foliar water. Although the tuber yields corresponded well to increases in the percentage ground cover, they did not correspond to the plant N status. All foliar N applications ameliorated the PCN-induced N deficits, seen at 58 DAP, and had significantly increased the plant N concentrations by 98 DAP. Why the 2% foliar N application did not benefit tuber yield is therefore unclear. However, the total numbers of tubers found in this treatment at harvest were substantially lower than with the 4 and 6% foliar N treatments, suggesting that the 2% N application was insufficient to maintain plant growth and prevent resorption of the tubers formed (Gunasena, 1969). Furthermore, as the ground cover in the 2% foliar N treatment declined faster than seen in the 4 and 6% foliar N treatments, a delayed tuber initiation or tuber bulking, which can occur from increased N availability but which also requires extended leaf area duration from which to gain a yield benefit (Harris, 1978), may have resulted in no yield benefit from the 2% N application.

Applying a single early foliar P application with, or instead of, the first foliar N application of a five foliar nutrient application programme, produced varying results. When foliar P was applied at 3.4% P, without foliar N, it caused serious leaf injury and ground cover was reduced, as found by Barel & Black (1979a) and Okuda & Yamada (1962), and which ultimately reduced tuber yield. When foliar P was applied alone at only 1.7%, or was included with the foliar N at 1.7 or 3.4% P, however, the ground cover was greater than where foliar N had been applied alone, which agrees with known responses to P applications (Dyson & Watson, 1971). These ground cover increases, which corresponded to tuber yield increases, may have resulted from amelioration of the PCN-induced N and P deficits seen at 61 DAP, and would agree with the suggestion by Trudgill (1980) that the lower growth rate of PCN-infected plants could be due to the reduced uptake of N and P. The investigation suggested, however, that tuber yield and tolerance benefits seen from applications of five 4% foliar N applications within the other experiments could benefit from either replacing the first foliar N application with 1.7% foliar P, or by including 3.4% foliar P within the first foliar N application of a five foliar N application programme.

When supplementary P was applied either as granules in the seedbed at planting or as foliar applications to early post-emergent plants, however, plant growth appeared to be reduced, in contrast to the later applications in the 1996 and 1997 experiments. Increasing the quantity of granular P at planting should have increased plant growth (Lewis, 1994), in the absence of nematodes, even with a soil P index of 5.0, as shown by Birch *et al.* (1967). Therefore, a negative N and P interaction may have occurred, influenced by soil type (Boyd & Dermott,

1967) or the high soil pH and high soil P index (as found in these experiments) may have adversely affected plant growth, as highlighted by Holliday (1963). Nutrient analyses of field grown plants at 30 DAP, however, showed that PCN infection had significantly reduced N and K concentrations within the plants but not the P concentration, adding further weight to the suggestion that P alone is not the most limiting nutrient in PCN-infected plants during this early growth period. However, the P concentrations within PCN-infected plants grown in the glasshouse were significantly increased by foliar P applications, well above those within plants from oxamyl treated pots, but the growth of these plants was less than that of plants from the oxamyl treated pots, in contrast to the findings of Villagarcía and Franco (1984) but in some agreement with the findings of Trudgill (1980). Applying supplementary P alone at early post-emergence was, therefore, detrimental to the growth of PCN-infected plants and, with the requirement of N for leaf expansion (Vos & Biemond, 1992), a reduced uptake of N may have prevented any responses to foliar P applications. Furthermore, it is also suggested that, along with other indicators (discussed in previous chapters), a separate mechanism (i.e. phytohormone imbalance) may have influenced the response of PCN-infected plants to the supplementary nutrients.

7.1.4 Plant nutrient status, its definition, and the effects of PCN

The overall findings of this research support the findings of others (e.g. Trudgill *et al.*, 1975a; Trudgill *et al.*, 1975b; Fatemy & Evans, 1986a; de Ruijter, 1998) in that concentrations of N, P and K within plants are reduced by PCN infection. In addition, however, it was also shown that, when plant samples were taken later in the season, the N and P concentrations were significantly higher in heavily infected plants than within lightly infected plants. This disputes the suggestion by Haverkort *et al.* (1994) that an inadequate N supply in the latter part of the season limits plant growth, but may suggest that the extensive root growth that occurs at this time, also shown by Haverkort *et al.* (1994), was conducive to a greater nutrient uptake in PCN-infected plants. However, although the nutrient concentrations were shown to be significantly affected by PCN invasion of the roots, their classification as 'sufficient' or 'deficient' by comparison to cited values (Piggott, 1986; Bennett, 1993; Walworth & Muniz, 1993) was ambiguous. Bennett (1993) gives general values which can apply throughout the season, whilst Piggott (1986) and Walworth & Muniz (1993) give specific values for specific plant parts at specific sampling dates. In addition, because the cited values change dramatically between sampling times, selecting an earlier or later time with which to make the comparison could suggest either a deficiency or an excess of any chosen nutrient. Where nutrient ratios were used as an alternative diagnostic tool, however, the findings generally agreed with the statistical comparisons but also defined which nutrient was most limiting and, in addition, suggested nutrient limitations which were not shown by cited sufficiency or deficiency values. As no remedial nutrient applications were used to rectify nutrient limitations suggested by the nutrient ratios, however, the usefulness of this method remains speculative for PCN-infected plants.

7.1.5 Plant nutrition and/or phytohormone interactions

Phytohormones, which have essential roles in the normal regulation and growth of all higher plants, are also produced in response to abnormal environmental conditions. Inadequate supplies of moisture or N to the roots, for instance, can induce the production and transport of abscisic acid (ABA) from roots to the shoots. As ABA can inhibit cell extension (Marschner, 1995), this would reduce plant growth until the moisture or N supply is again adequate to support further growth. PCN have been shown to reduce N uptake and, as Fatemy *et al.* (1985) have shown, increase the levels of ABA within plants, so reduced growth of PCN-infected plants may be caused by the inhibitory effects of ABA. Where supplementary foliar N was applied to plants heavily-infected with PCN within my experiments, however, the N deficit was redressed and would, therefore, return the plant N status to adequate. Consequently, the stress induced production of ABA should have been reduced and the restriction on plant growth removed, so that a reasonable yield could be expected. The timing of the first foliar N application (tuber initiation), however, would have been too late to redress the pre-tuber initiation N deficit and the poor ground cover would have restricted any subsequent potential yield benefits. Equally feasible, however, is that the main production sites of cytokinins (CYT) are meristematic root tissue (Davies, 1995) and, as this coincides with the main entry point of PCN, the production of or the growth promoting role of CYT may well be disrupted by PCN invasion. Therefore, the influence and potential growth limiting aspects of CYT production within PCN-infected plants may also warrant further investigation.

7.1.6 Methods and designs of experiments

Field experimentation was chosen as the main type of investigation for this research as the small quantity of work previously carried out in this area highlighted how contradictory results can occur between field and glasshouse studies, e.g. the findings of Trudgill (1980). Field experimentation also allows for the use of destructive plant analysis (e.g. root invasion analysis) without compromise to the CVs , and also allows the experiment to continue for final yield and tolerance assessments of the treatments. One of the difficulties of using field sites to investigate plant and PCN interactions, however, is that of finding uniform PCN population densities. This can be difficult, as PCN normally develop from foci within fields (Haydock & Evans, 1994). However, in all of these field experiments, despite the high CVs which may have been due to variable PCN population densities, the lack of statistical differences between treatment means imply that the populations were relatively uniform. PCN population densities within the 1996 experiments were quite low, with means of 13 and 19 eggs/g soil, but they were sufficient to reduce tuber yields in plots not treated with oxamyl by up to 10%, in agreement with the findings of Whitehead *et al.* (1984) and Trudgill *et al.* (1983), and thus to show tolerance benefits from treatment applications. In 1997 and 1998, however, greater PCN population densities were used (means of 85 and 34 eggs/g soil respectively) to further stress the potato plants. Potato cultivars were chosen in each year on the basis of their tolerance as demonstrated by other researchers: Pentland Dell (Trudgill *et al.*, 1983; Whitehead *et al.*, 1984), Santé (Haydock *et al.*, 1996) and Estima (Whitehead *et al.*, 1987). It was hoped that the use of these cultivars would prevent total crop loss whilst allowing the plants to be stressed.

The split-plot experiment design used in 1996 was originally chosen as the most suitable method to allow the comparison of foliar treatments over plots that were sub-divided for nematicide and non-nematicide treatment. This design is useful where small plots are not practical (Mead *et al.*, 1993) as it can reduce the influence of soil type, soil nutrient and pest incidence variability which can occur in large experiments. However, this design lacked sensitivity when comparisons between nutrient and oxamyl applications were required. To overcome this problem, the 1997 and 1998 experiments were based on the 'analysis of planned orthogonal contrasts'. This experiment design is much under-used but is a very powerful statistical analysis method (Pearce, 1992a, 1992b) which provides simple, factorial and dose response analysis, which few other single designs can achieve. In addition to the analysis of variance methods and simple linear regressions, linear regressions for blocked experiments were also employed. This method removes the effects of experiment 'blocking', which simple linear regressions do not, and is, therefore, more suitable when analysing for linear trends within blocked experimental data (personal communication, K. Vines, Open University statistical advisor). In addition to these statistical techniques, the use of PCN initial population densities as a covariate to remove underlying PCN pressure differences between treatments was also considered for use with the experiment data. Although there is a large body of evidence to show the strong correlation between initial PCN population density and final tuber yield, this is not always the case (Brown, 1983). Furthermore, where a treatment application within an experiment, e.g. a nematicide, effectively reduces the PCN pressure from that of the sampled estimate, the estimated PCN population density value is invalidated. Therefore, root invasion data, which provides an accurate representation of PCN pressure and also follows the rules of covariance (Gomez & Gomez, 1984), is suggested as a more suitable covariate for PCN experiments which include treatments employed to manipulate PCN population densities.

7.2 Conclusions

It is unlikely that, with the weight of evidence from this and other research, the simple deficiency of N, P or K is responsible for the major yield loss associated with PCN. It is possible that deficiencies of other nutrients could be affecting the plant's ability to respond to applications of N, P and K but further research into this would be required. The complex nature of the interactions between the nutrients, as shown by nutrient ratios, could mean that as soon as one limitation is overcome other nutrients become limiting. However, this research has demonstrated that supplementary foliar N, P and K can improve plant tolerance of PCN invasion, but that only small improvements in growth and yield can be achieved. Where field and glasshouse investigations were compared, plant responses to applied fertiliser were similar but the uptake of foliar P and the efficacy of the nematicide were affected, thus highlighting the greater suitability of field experimentation for these types of investigations.

7.2.1 The effects of fertiliser application method on plant PCN tolerance

Although the placement of liquid fertilisers did give some benefits to plant growth and yield, these were not significant and could not be judged to improve the plant's tolerance of PCN attack. However, the method of fertiliser application experiment was carried out on a soil of low initial PCN population density and, therefore, further work is necessary to clarify whether the more efficient liquid placed fertilisers would be of greater or lesser benefit to plant growth at higher levels of PCN soil infestation. Applying one third of the basal seedbed fertiliser with foliar NPK applications was an effective replacement for the normal seedbed application, increasing the nutrient concentrations within the plants and giving equivalent or higher tuber yields than where all of the fertiliser was applied to the seedbed. Foliar N, P and K applications are, therefore, a realistic alternative for the supply of these nutrients to PCN-infected potato plants.

7.2.2 Timing of broadcast granular N applications

Applying all or most of the recommended quantity of N in the seedbed at planting can increase the N concentrations within PCN-infected plants and, therefore, reduce the PCN-induced N deficits. The increased N concentration, however, did not promote plant growth over that seen in PCN-infected plants receiving only half of the recommended N in the seedbed at planting. It is very important to supply N at planting and tuber initiation, especially on light free-draining soils, and, where this is supplemented by foliar N, yield improvements of PCN-infected plants can be achieved.

7.2.3 Application timing and quantity of foliar N, P and K

Applying supplementary foliar N as a 4% solution, commencing at tuber initiation and then at approximately 14-day intervals, gave small but consistent ground cover, leaf area index, tuber yield and, therefore, tolerance benefits to PCN-infected plants. Decreasing the solution concentration to 2% N gave no benefit, whilst increasing the concentration to 6% N gave only a small additional benefit to the tolerance of PCN-infected plants. Applying foliar P at 3.4%, commencing at tuber initiation and then at approximately 14-day intervals, gave early ground cover improvements but hastened crop senescence and thus reduced tuber yields. However, when one foliar P application was made at tuber initiation, either alone at 1.7% P or with 4% N at 1.7 or 3.4% P, ground cover and yields were greater than with foliar N alone. In addition, supplementary P applied as granules in the seedbed at planting or as an early post-emergence foliar application, appeared to be detrimental to the growth of PCN-infected plants, although applying it to the foliage did increase the P concentration within the plant. Foliar N applied with foliar K, commencing at tuber initiation and then at approximately 14-day intervals, increased the yield and tolerance of PCN-infected plants to a similar level to that of foliar N alone. However, although many of the foliar applications increased the concentrations of the nutrients within plants, few real plant growth benefits occurred. The use of foliar N, P and K applications can benefit the tolerance of PCN-infected plants but further research is needed to investigate further the most suitable combinations and application timings.

7.2.4 Plant nutrition, plant growth and phytohormone interactions

All plants heavily-infected by PCN had much reduced growth, extreme in 1997, and this showed as retarded plant emergence, leading to poor early season ground cover and radiation interception and, ultimately, greatly reduced yields. PCN-infection also greatly reduced the concentrations of N, P and K within potato plants but, although they were significantly affected, they could not be classed as deficient with any degree of certainty. However, nutrient ratios and statistical comparisons suggested that (of the three nutrients investigated) the nutrients most limiting plant growth were: K and N at 30 DAP, P and K and possibly N at 56 to 82 DAP, and K at 104 to 107 DAP; whilst cited values suggest N and K at 56 to 82 DAP, and P and K at 104 to 107 DAP. The identification of nutrient deficiencies using conventional techniques was shown to be problematical where comparisons to published sufficiency ranges were made and often inconclusive using statistical analysis. The use of nutrient ratios, however, not only overcame these problems but provided information of the nutrient requirement order and, where the nutrients were shown to be sufficient or in excess, nutrient ratios still identified the imbalance and specified nutrients potentially limiting crop growth. However, as no relationships could be shown between the nutrient ratios and tuber yields, and no remedial applications were based on the findings, their value is unsupported. Although nutrient concentrations in plants heavily infected by PCN were increased to similar or higher levels than those in lightly-infected plants, no real plant growth or yield improvements were seen, leading to speculation that phytohormones may be limiting the plant responses to foliar applied nutrients.

7.3 Further research

As there were 14 day intervals between foliar applications, this may not have been sufficient to mimic the normal nutrient uptake of the plant roots and, therefore, shorter intervals between applications may be more beneficial. In addition, because it was shown that the application of nutrients to early post-emergent plants was possible, a comprehensive investigation of combined nutrient applications at this time may determine if the production of early ground cover can be stimulated, thus reducing this yield limitation. Foliar applications may also be more useful if they are applied on the basis of results of plant nutrient analysis and, calculation of nutrient ratios. However, there is still a need for very intense sampling, throughout the whole season, to determine how nutrient concentrations change within PCN-infected plants, and this needs to include as many nutrients as possible. There is also a need to investigate further the role of phytohormones within PCN-infected plants as their association with nutrients and water stress could be of great importance.

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Appendix 1. Papers and abstracts published from this thesis

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